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Understanding the immediate and time-delayed effects of deforestation on biodiversity in the Gran Chaco

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Abstract

Land-use change is a primary driver of biodiversity loss. During recent decades, the tropics and subtropics have witnessed accelerating deforestation rates, resulting in widespread local extinctions. Even if further deforestation was to be avoided, species would likely continue to disappear due to delays in their responses to habitat transformation. The overarching goals of this thesis were to provide a better understanding of the effects of past and contemporary land use on biodiversity in the Argentine Dry Chaco, and to develop approaches that capture the impacts of land-use change on biodiversity before local extinctions occur. The Argentine Dry Chaco provides an excellent scenario for this purpose due to its dynamic land-use history, the high deforestation rates the region has experienced recently, and its high levels of biodiversity. At the community level, I found that species richness of birds and mammals was greatly influenced by past landscape patterns, suggesting time-delayed responses to land-use change and the evidence of an extinction debt. A novel, spatially explicit approach showed that areas recently converted to agriculture had highest extinction debt. The time-delayed responses to land-use change were due to habitat fragmentation rather than habitat loss. At the population level, I used occupancy models to obtain spatial proxies of population change, using the threatened giant anteater as an example. Anteater occupancy decreased particularly after 2000 when rapid agricultural expansion occurred. My results further suggested that land-use change had substantial indirect effects on species' populations. Finally, I assessed the effects of deforestation on collared peccaries at the population and individual level by combining occupancy models with indices of physiological stress. Peccary occupancy was highest in areas with high woodland cover. Where peccaries were present, physiological stress was negatively correlated with food availability, but not with predictors related to deforestation. Overall, this thesis shows that deforestation is driving species to extinction in the Argentine Dry Chaco. While some species may disappear quickly following deforestation, extinctions of other species may not be immediate, thus providing an opportunity to prevent those extinctions. The approaches presented in this thesis help to identify those opportunities in dynamic landscapes such as deforestation frontiers that emerge to meet the rising demand for agricultural products.

Zusammenfassung

Landnutzungswandel ist eine der Hauptursachen von Biodiversitätsverlust. In den Tropen und Subtropen führt eine Ausweitung von Agrarflächen zu einer vermehrten Abholzung der Wälder. Selbst wenn zukünftige Waldrodung vermieden werden kann, ist ein weiterer Artenrückgang sehr wahrscheinlich, da Tiere oft zeitverzögert auf Veränderungen reagieren. Die Hauptziele dieser Arbeit waren die Effekte von vergangener und aktueller Landnutzung auf Biodiversität im argentinischen Chaco besser zu verstehen und Ansätze zu entwickeln, die die Auswirkungen von Landnutzungswandel auf Biodiversität erfassen, bevor ein lokales Aussterben auftritt. Der argentinische Chaco ist durch seine lange Geschichte an Landnutzung, den hohen Abholzungsraten in den letzten Jahrzehnten und der hohen Biodiversität bestens für solche Untersuchungen geeignet. Auf Ebene von Artengemeinschaften habe ich herausgefunden, dass der Artenreichtum von Vögeln und Säugetieren stark durch vergangene Landschaftsmuster beeinflusst wurde, was auf zeitverzögerte Reaktionen auf Landnutzungswandel hindeutet, sowie darauf, dass ein Teil der momentan vorkommenden Arten aufgrund von vergangenen Landnutzungsänderungen noch aussterben wird. Ein neuer, räumlich expliziter Ansatz konnte zeigen, dass kürzlich in Agrarland umgewandelte Flächen die höchste Wahrscheinlichkeit für lokale Aussterbeereignisse aufweisen. Die zeitverzögerten Reaktionen auf Landnutzungswandel fanden hauptsächlich aufgrund von Fragmentierung von Lebensraum statt, mehr noch als durch Lebensraumverlust. Auf Populationsebene habe ich Vorkommens-Modelle für Ameisenbären benutzt, um regionale Populationswandel zu untersuchen. Das Vorkommen von Ameisenbären ist seit 1985 stark zurückgegangen, besonders nach 2000, als die Ausweitung von Agrarflächen besonders stark zunahm. Außerdem legen meine Ergebnisse nahe, dass Landnutzungswandel starke indirekte Effekte auf Wildtierpopulationen hat. Abschließend habe ich die Effekte von Abholzung auf Halsbandpekaris auf Populations- und Individuen-Ebene untersucht, indem ich Vorkommens-Modelle mit physiologischen Stressindizes kombinierte. Die meisten Pekaris kamen in abgelegenen Regionen mit hohem Waldanteil vor. Dort wo Pekaris vorkamen, war ihr physiologischer Stress negativ mit der Verfügbarkeit an Nahrung korreliert, jedoch nicht mit Abholzung. Insgesamt betrachtet zeigt

diese Arbeit, dass das Abholzen von Wald zu einem Aussterben von Arten im argentinischen Chaco führt. Während manche Arten nach dem Abholzen wahrscheinlich schnell verschwinden, kann es sein, dass andere Arten nicht direkt aussterben, was wiederum ein Zeitfenster für Naturschutzmaßnahmen eröffnet, um diese Aussterbe-Ereignisse noch zu verhindern. Die hier vorgestellten Ergebnisse können dabei helfen solche Zeitfenster zu identifizieren, welche in dynamischen Landschaften entstehen, wie zum Beispiel Abholzungsgebiete die entstehen um den steigenden Bedarf an Agrarprodukten zu decken.

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Introduction

1 The global biodiversity crisis

Human activities have transformed the Earth's surface at least since the Pleistocene (Ellis *et al.* 2013). Throughout the last three centuries, the pressure exerted by humans on the global environment has increased drastically, exceeding some of the biophysical limits of our planet and leading to irreversible environmental changes (Rockström *et al.* 2009; Zalasiewicz *et al.* 2011; Steffen *et al.* 2015; Crutzen 2016). As a result, a new human-dominated epoch has emerged, the Anthropocene (Lewis & Maslin 2015; Crutzen 2016). In this era of human-induced global change, the loss of biodiversity is considered one of the most severe environmental concerns (Ceballos *et al.* 2015), with growing empirical evidence confirming it. For example, studies have shown that species extinction rates have sharply increased over the last two centuries, and as a result, current documented extinction rates are orders of magnitude higher than pre-human background rates (Ceballos *et al.* 2015). This suggests that a sixth mass extinction is under way (Barnosky *et al.* 2011; Ceballos *et al.* 2015). Additionally, the last IPBES Global Assessment estimated that out of the ~8.1 million animal and plant species inhabiting the Earth (Mora *et al.* 2011), around 1 million are threatened, with many facing extinction within decades (Díaz *et al.* 2019)

Biodiversity loss is often assessed by documenting species extinctions (Barnosky *et al.* 2011; Dirzo *et al.* 2014). It is estimated that 200 species of vertebrates have gone extinct during the last 100 years, representing a loss of about 2 species per year (Ceballos, Ehrlich & Dirzo 2017). However, the situation is even more worrisome when looking at population extinctions, as the rates at which populations disappear are much higher than the rates of the entire species becoming extinct (Ceballos & Ehrlich 2002; Ceballos, Ehrlich & Dirzo 2017). For instance, Hughes, Daily and Ehrlich (1997) suggested that approximately 16 million populations are going extinct every year in tropical forests, and Ceballos and Ehrlich (2002) estimated that the populations of most species have been reduced by 50-100%. This means that by focussing on species extinctions, we may underestimate the severity of the current biodiversity crisis (Ceballos, Ehrlich & Dirzo 2017). In addition, the extinction of a species' population (or even a population decline) can lead to the extinction of other species in the community, thus having severe effects on the entire ecosystem. In such cases, the species is considered as functionally extinct, even though it has not disappeared yet (Säterberg, Sellman & Ebenman 2013). Finally, while documenting the extinction of species can help to understand the magnitude of species extinction rates or to identify threats to biodiversity, it

is not enough to save species from extinction. In the face of the current biodiversity crisis, there is an urgent need to develop approaches that help to detect potential species extinctions early on, in order to save species otherwise doomed to extinction.

Land-use change, overexploitation, climate change and invasive species are considered as main threats to biodiversity (Maxwell *et al.* 2016; Grooten & Almond 2018). Among these threats, land-use change has exerted the largest negative impact on terrestrial nature since the 1970's (Díaz *et al.* 2019), and is currently considered to be one of the main threats to biodiversity (Maxwell *et al.* 2016; Tilman *et al.* 2017; Mazor *et al.* 2018). In particular, agricultural activities, mainly cropping and livestock grazing, have been reported as one of the main drivers of biodiversity loss (Maxwell *et al.* 2016). Indeed, 62% of the species listed as threatened or near-threatened by the IUCN, are threatened by agricultural activities (Maxwell *et al.* 2016).

About three quarters of the Earth's surface is significantly altered, and one quarter of the land has already been transformed into cultivated land (Millennium Ecosystem Assessment 2005; Díaz *et al.* 2019). Unfortunately, the use of land by humans is likely to increase in the future to sustain the ever-growing human population; it is estimated that around 10 billion people will live on the Earth by the end of the century (Gerland *et al.* 2014). This, together with the even more damaging expected increase in the global consumption of land-based products (Tilman *et al.* 2011), suggests that transformation of natural ecosystems through the expansion of agriculture will continue with substantial consequences for biodiversity. Mediterranean forests and temperate grasslands have been the ecosystems most affected by agriculture expansion (Millennium Ecosystem Assessment 2005). With more than half of the temperate regions already transformed, land conversion is now focused on the tropics and subtropics, which contain the highest levels of biodiversity on the planet (Millennium Ecosystem Assessment 2005; Hansen *et al.* 2013; Díaz *et al.* 2019). The tropical and subtropical dry forests of South America have suffered the highest deforestation rates due to agriculture expansion (Hansen *et al.* 2013; Curtis *et al.* 2018).

Tropical and subtropical dry forests and savannas make up more than 40% of all tropical and subtropical forests (Figure I-3), are important for global net primary productivity and carbon storage, sustain hundreds of millions of livelihoods, and harbour a rich and unique biodiversity (Murphy & Lugo 1986; Janzen 1988; Field *et al.* 1998; Miles *et al.* 2006; Baumann *et al.* 2011; Cao *et al.* 2016; Pennington, Lehmann & Rowland 2018). Despite the ecosystem services this biome provides, dry forests are disappearing rapidly (Hansen *et al.*

2013). This is because these biomes contain much of the world's last undeveloped land, still suitable for different cropping systems, making them vulnerable to agricultural expansion (Miles *et al.* 2006; Lambin *et al.* 2013). The South American tropical dry forests have particularly been affected by agricultural expansion (Hansen *et al.* 2013), threatening the high biodiversity that these forests harbour (Miles *et al.* 2006). Moreover, a relatively small proportion of tropical dry forests are under protection (Miles *et al.* 2006; Pennington, Lehmann & Rowland 2018). As a result, tropical and subtropical dry forests are considered one of the most threatened biomes in the world, yet, they remain neglected and under-researched (Janzen 1988; Miles *et al.* 2006). This is partly due to rain forests having received much of the attention directed towards conservation and research, despite the high vulnerability of tropical dry forests in comparison to rain forests (Pennington, Lehmann & Rowland 2018). For instance, while the Amazonian rain forests is about 80% intact, less than 10% of tropical dry forests in Latin America remains (Pennington, Lehmann & Rowland 2018). In addition, South American tropical dry forests have experienced the highest rates of forest loss in the world, due to deforestation in the Gran Chaco (Hansen *et al.* 2013). Therefore, there is an urgent need to increase our understanding of the effects of land-use change on biodiversity in tropical dry forests.

2 Biodiversity responses to land-use change

Land-use and land-cover change cause the loss, fragmentation and degradation of habitat (Foley *et al.* 2005; Haddad *et al.* 2015) (Figure I-1). When habitat loss occurs, the amount of area available for a species is reduced, resulting in the decline in the abundance of that species. Additionally, the fragmentation of the remaining area often increases (Fahrig *et al.* 2019), influencing the population dynamics of a species, for example by decreasing the dispersal among habitat patches (Hanski 1998; Hanski 2015). This is because habitat fragmentation results in the division of large and continuous habitats, into smaller and isolated habitat patches, i.e., fragmentation (Saunders, Hobbs & Margules 1991; Ewers & Didham 2006). Additionally, edge effects, i.e., interactions between two adjacent ecosystems that are separated by an abrupt transition (edge), increase in fragmented landscapes (Murcia 1995).

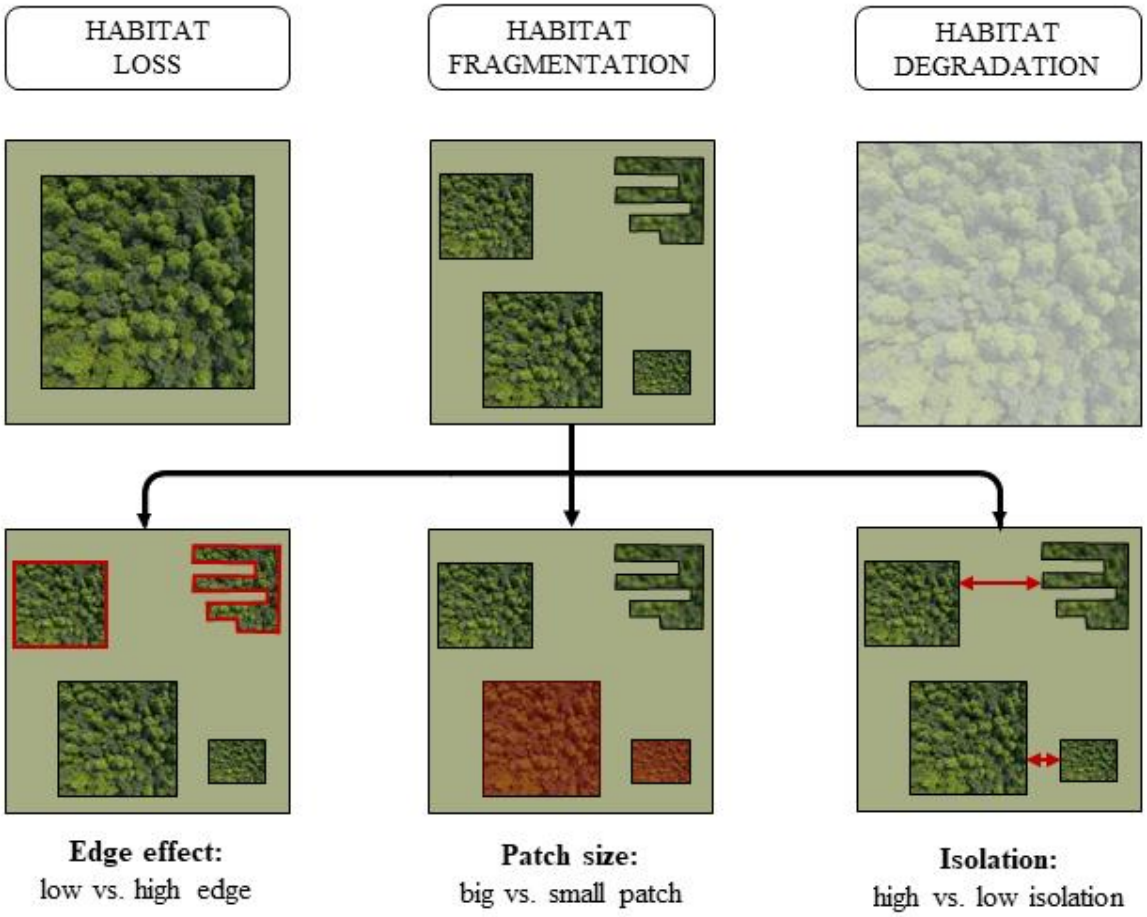

Figure I-1: Simplified illustration of the effects of habitat loss, fragmentation and degradation in the landscape. Habitat loss reduces the amount of area available for a species. Habitat fragmentation modifies the spatial configuration of the remaining area in the landscape: a fragmented landscape contains more, smaller and isolated patches and a larger proportion of edge effect. Finally, habitat degradation reduces the quality of the habitat, while maintaining the amount of habitat area and the spatial configuration of the former landscape.

Both habitat loss and fragmentation have been considered to harm biodiversity for decades (Miller-Rushing *et al.* 2019). However, recent studies have questioned the negative effects of fragmentation and have proposed that the amount of habitat in the landscape is the main driver of biodiversity loss (Fahrig 2013; Melo *et al.* 2017). Yet, empirical studies continue to demonstrate the negative effects of habitat fragmentation on different taxa, including mammals (Crooks *et al.* 2017; Zimbres, Peres & Machado 2017), birds (Blandón *et al.* 2016), reptiles and amphibians (Russildi *et al.* 2016; Schneider-Maunoury *et al.* 2016) and plants (Lindgren & Cousins 2017). Regarding biomes, while some studies have shown that the negative effects of fragmentation are stronger in the tropics than in temperate regions (Lindell *et al.* 2007), others have found that biodiversity responds mostly positively regardless of biome (Fahrig 2017). Yet, most studies that have assessed the effects of fragmentation on biodiversity at the landscape level have largely focused on temperate regions (Fahrig 2017). This disagreement among studies indicates that understanding the

effects of habitat fragmentation on biodiversity is not straightforward, and that several factors can mask such effects (Ewers & Didham 2006). For example, the long-term effects of fragmentation have rarely been considered when disentangling the effects of habitat loss and habitat fragmentation, and therefore, it is poorly known whether species´ extinctions occur immediately after habitat transformation or not (Ewers & Didham 2006; Fletcher Jr *et al.* 2018; Fahrig *et al.* 2019). Therefore, it is crucial to consider both the short-term and long-term effects of habitat loss and fragmentation on biodiversity to properly assess the consequences of land-use change.

Biodiversity is often threatened by multiple factors. From the almost 9,000 threatened species assessed by Maxwell *et al.* (2016), 80% were found to be affected by more than one threat. In addition, these multiple threats can interact. The term synergistic effect is used to describe such interactions between threats, and it refers to the simultaneous actions of several threats that have a larger effect on biodiversity than the sum of the isolated ones (Brook, Sodhi & Bradshaw 2008). However, despite the importance of these synergies, threats are often studied in isolation (Mazor *et al.* 2018). Interactions between land-use change and other threats such as hunting, invasive species or climate change have previously been reported, with land-use change and hunting often interacting in tropical deforestation frontiers (Cullen Jr, Bodmer & Pádua 2000; Brashares, Arcese & Sam 2001; Carroll 2007; Didham *et al.* 2007; Jetz, Wilcove & Dobson 2007; Mora *et al.* 2007; Romero-Muñoz *et al.* 2019). Land-use change directly affects species´ populations through habitat loss and habitat fragmentation, in addition, important indirect effects can occur (Brook, Sodhi & Bradshaw 2008). For example, habitat fragmentation is known to lead to an increase in human pressure as forest fragments become more accessible, thus increasing hunting pressure or fire risk (Brook, Sodhi & Bradshaw 2008). When a landscape becomes fragmented, the amount of edge increases and hunters can easily access the core area of the forest where animals shelter from humans (Corlett 2007). Additionally, increases in road density due to fragmentation facilitates access to areas that were previously isolated (Laurance, Sayer & Cassman 2014). Therefore, understanding how land-use change may affect species´ populations both directly and indirectly (e.g., through high hunting pressure or fire risk in fragmented landscapes) is crucial in order to get a more thorough picture of the impact of land-use change on biodiversity.

3 Time-delayed responses to land-use change

The impact of land-use change on biodiversity has received considerable research attention (Mazor *et al.* 2018). However, most research treats land-use change as a static process, where the effects of land use composition and configuration on biodiversity are assessed at one point in time (Jung *et al.* 2019). This ignores the fact that land-use change is a continuous process occurring over many decades (Ewers *et al.* 2013). Most importantly, the effects of land-use legacies on biodiversity have often been neglected, where it is erroneously assumed that the habitat amount and fragmentation at the time of biodiversity sampling are the only factors affecting biodiversity (Ewers & Didham 2006; Fletcher Jr *et al.* 2018). This may lead to erroneous conclusions, as historical land-use patterns influence biodiversity substantially (Kuussaari *et al.* 2009; Metzger *et al.* 2009; Krauss *et al.* 2010). This is because the impact of land-use change on individuals is not limited to the immediate impact, and there is often a time delay between landscape transformation and species extinction (Kuussaari *et al.* 2009; Essl *et al.* 2015). Extinction debt represents such delay in the extinction of species and is defined as the number or proportion of extant species predicted to go extinct due to past landscape transformation (Tilman *et al.* 1994).

Predicting where and when such extinction debt is more likely to be paid may help to avoid the expected future loss of species and therefore, provides an essential window of opportunity for averting biodiversity loss (Kuussaari *et al.* 2009). There are four main benefits of better understanding extinction debt. First, estimating when species' communities are more likely to reach a new equilibrium after landscape transformation (i.e., the time delay to extinction) gives insights into how much time there is left before local extinctions occur. Second, predicting where local extinctions are more likely to occur highlights areas where conservation efforts should be targeted to avoid those extinctions. Third, determining the main driver of the time delay to extinction may help to decide which type of conservation activities may be more effective. Finally, assessing biodiversity loss without considering time-delayed responses may underestimate the consequences of land-use change on biodiversity, as the actual number of species under threat will be underestimated, especially in regions where extinction debt is large (Hanski & Ovaskainen 2002; Kuussaari *et al.* 2009). Therefore, understanding extinction debt allows us to know *when* extinctions might occur, *where* and *why* extinctions are likely to occur, and *how bad* it will be once the extinction debt is paid.

Despite the importance of identifying extinction debt for conservation planning, relatively few studies have assessed the effects of time-delayed responses to land-use change on biodiversity (Lira, de Souza Leite & Metzger 2019). Moreover, the majority of these studies have been carried out in grassland and temperate forests (Figueiredo *et al.* 2019; Lira, de Souza Leite & Metzger 2019), where broad-scale landscape transformation mainly occurred before 1950 (Millennium Ecosystem Assessment 2005). This suggests that an eventual extinction debt in such regions is likely to already have been paid for many species. In fact, extinction debt in those regions has primarily been reported for long-lived species such as plants (Lindborg & Eriksson 2004; Helm, Hanski & Pärtel 2006; Krauss *et al.* 2010; González-Varo *et al.* 2015), suggesting that local extinctions in short-lived species may have already occurred. In contrast, the tropics and subtropics have recently experienced extensive landscape transformation, and as a result, extinction debt is more likely to be unpaid (Hanski & Ovaskainen 2002; Lira, de Souza Leite & Metzger 2019). Thus, in order to counteract future local extinctions in such dynamic landscapes, it is crucial to gain understanding of time delays between land-use change and species' responses.

4 The impacts of past and contemporary deforestation at multiple levels of organization

Forests cover about one-third of the globe's terrestrial surface, and provide habitat for about three quarters of terrestrial biodiversity (CPF 2008). Understanding the effects of deforestation on biodiversity is therefore essential. Much of the research on this topic relies on relating species distribution models to landscape patterns (Elith & Leathwick 2009). This approach however, can only detect the effects of deforestation several years after it occurs due to the delay in species extinctions following deforestation (Kuussaari *et al.* 2009).

The effects of deforestation on species start with effects on individuals before they translate to the population level (Ellis, McWhorter & Maron 2012) (Figure I-2). An increasingly used approach to investigate the effects of environmental changes at the individual level is studying the physiological responses to those changes (Busch & Hayward 2009; Kumar & Umapathy 2019). Indeed, several studies have addressed the physiological responses to a range of disturbances caused by environmental change, such as hunting pressure (Gobush, Mutayoba & Wasser 2008), human disturbance (Walker, Dee Boersma & Wingfield 2006; Wasser *et al.* 2011), pollution (Wikelski *et al.* 2002) and changes in habitat availability and fragmentation (Martínez-Mota *et al.* 2007; Janin, Léna & Joly 2011; Cantarelli *et al.* 2017).

Stress hormone levels are commonly used to measure the physiological state of individuals (Möstl & Palme 2002). After an individual encounters a stressful situation such as deforestation, it triggers a physiological stress response by increasing stress hormone levels (Sapolsky, Romero & Munck 2000). Glucocorticoids are a class of hormones that are involved in the stress response, and their determination as metabolites in feces, i.e., fecal glucocorticoid metabolites (FGMs), provides a non-invasive measure to assess stress of individuals (Sheriff *et al.* 2011). Individuals can present chronically elevated levels of FGM when they do not adapt to the new environmental conditions following a disturbance such as deforestation (Romero 2004). This can have detrimental effects on the individual, by supressing the immune system and growth or inhibiting reproductive behaviour, thus compromising the survival of the animal (Wingfield & Ramenofsky 1999; Ellis, McWhorter & Maron 2012). As a result, population declines and subsequent local extinctions may occur (Figure I-2).

Population declines can persist over many decades before species go extinct (Hylander & Ehrlén 2013; Norris 2016), and identifying such declines may therefore provide an alternative approach for detecting species extinctions at an early stage (Pillay *et al.* 2011). This is particularly important for effective conservation planning, as different conservation measurements should be implemented depending on the population status of a species (Gilroy & Edwards 2017). In addition, identifying population declines rather than declines in the distribution of a species provides a better picture of an eventual risk, because population decline is a prelude of species extinctions (Ceballos & Ehrlich 2002; Ceballos, García & Ehrlich 2010). In fact, studies have reported declines in the abundance of species, but not in their distributions, suggesting the presence of extinction debts (Pillay *et al.* 2011). This highlights the need to develop approaches that help to predict population declines before populations reach critical thresholds and are driven to extinction.

An ongoing decline of populations and eventual extinction of a species can have consequences on the entire community. For instance, a number of studies have shown how habitat loss can have a great impact on species interactions, leading to the restructuring of the entire community (Tylianakis, Tscharntke & Lewis 2007; McWilliams *et al.* 2019). However, such impacts can take several years to manifest at the community level, due to the delay in the extinction of species following deforestation (Kuussaari *et al.* 2009). Therefore, it is also crucial to identify the impacts of deforestation at the community level, as well as its time-delayed responses, especially in human-dominated landscapes where humans and its activities can alter entire communities.

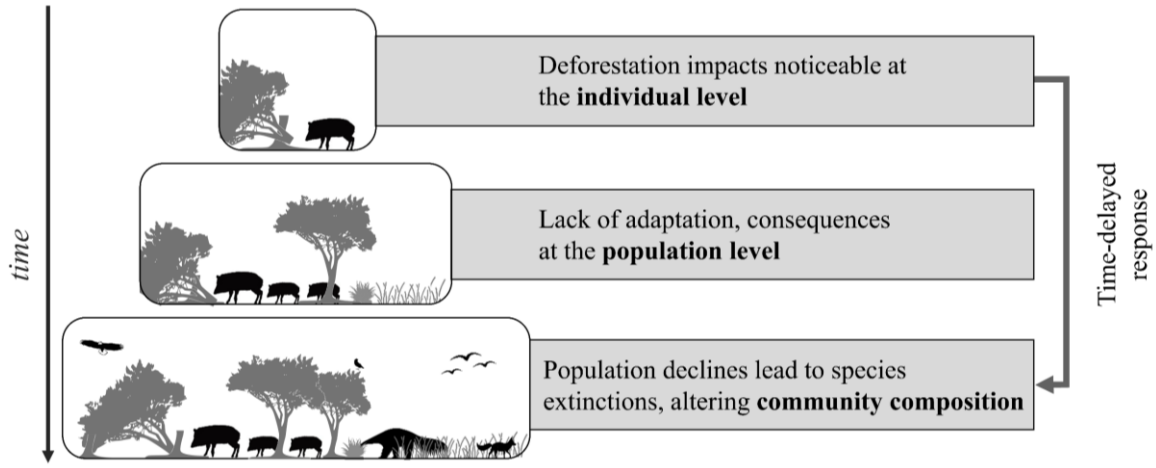

Figure I-2: Simplified illustration of the effects of deforestation on biodiversity at different levels of organization and over time. The impacts of deforestation are first noticeable at the individual level. If individuals do not adapt to the new environmental conditions following deforestation, population declines occur. Finally, low population densities can lead to the extinction of populations and eventually local extinction of species, thus affecting entire communities. The time span between deforestation (at this point effects are usually detected only by looking at the individual physiological state) and species extinctions is known as time-delayed response or relaxation time.

Investigating how land-use change affects biodiversity at different levels of organization can provide a better understanding of the impacts of land-use change, and help to detect those impacts at an early stage, before local extinctions occur (Figure I-2). This can be achieved by (1) identifying time-delayed responses to land-use change and its corresponding extinction debt (community level), (2) mapping population declines (population level) and (3) assessing the individual physiological state (individual level).

5 The Gran Chaco

The Gran Chaco, covering more than 1 million km^2, is the largest tropical dry forest in the world (Olson *et al.* 2001; Grau, Gasparri & Aide 2008). This ecoregion stretches across Argentina, Paraguay, Bolivia and a small proportion of Brazil (Figure I-3). The Chaco is characterized by a flat topography and a highly marked seasonal climate. Temperatures range from -7ºC in winter to almost +50ºC in summer (Prado 1993). Precipitation also varies greatly in the Chaco, with more than 70% of the rainfall occurring during the rainy season which takes places between November and April (Bucher 1982; Prado 1993), and is distributed along a precipitation gradient that results in the sub-division of the ecoregion. The Wet Chaco, occupying the eastern part, has an annual rainfall between 900 and 1200 mm and is the most productive sub-region. The western part, known as the Dry Chaco,

receives an annual rainfall between 450 and 700 mm. A transition area divides these two sub-regions constituting an ecotone between the dry and the wet zone (Cabrera & Willink 1973). Open dry woodlands are the dominant vegetation type, mainly consisting of xerophytic trees and shrubs (Bucher 1982). Other vegetation types such as grasslands and savannas also occur, however they constitute only a small proportion of the region (Bucher 1982; Baumann et al. 2017) (Figure I-3).

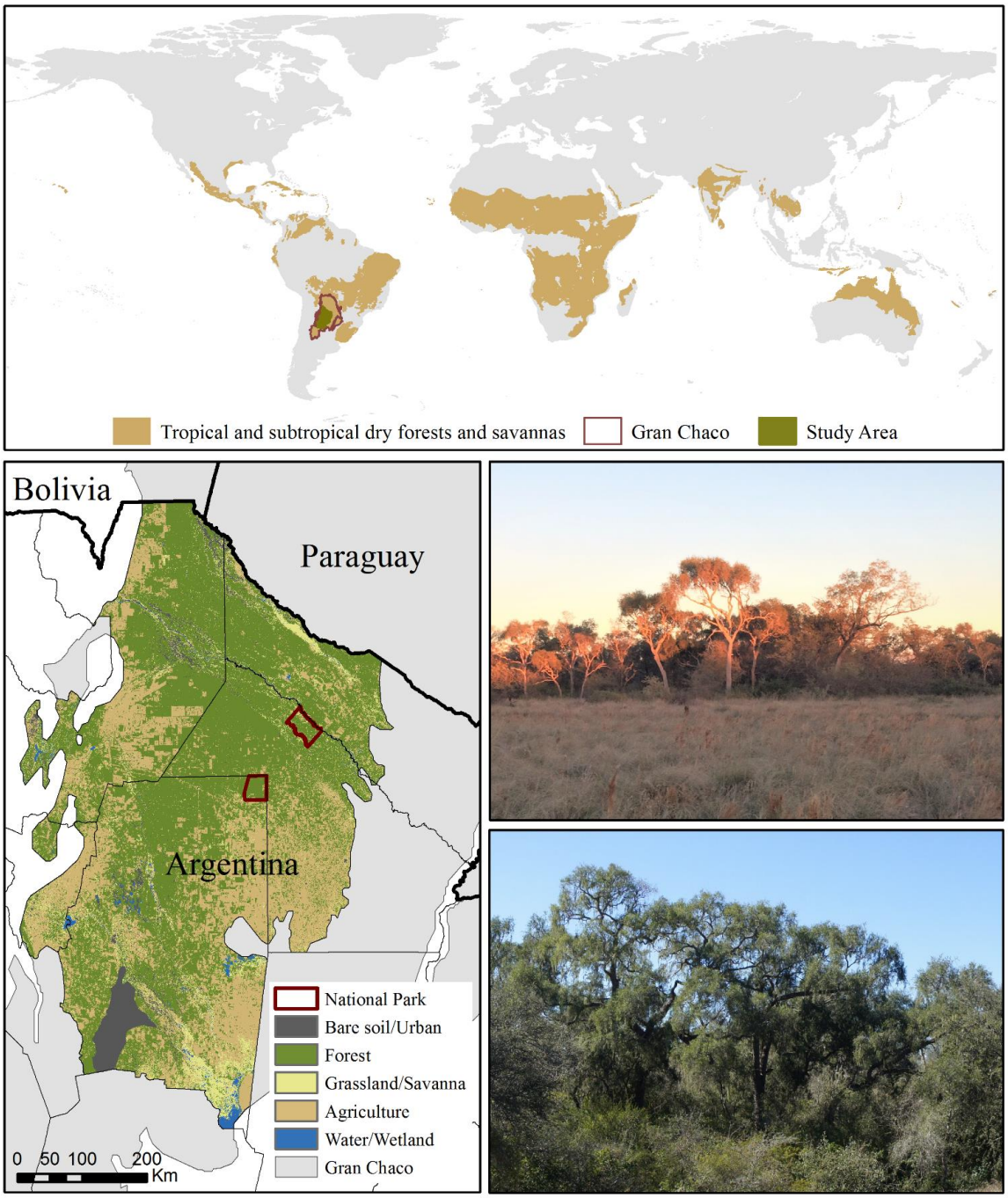

Figure I-3: Tropical and subtropical dry forests and savannas in the world (top map) and location of the study area in northern Argentina (bottom-left map). Lines in Argentina demarcate Argentine provinces. Photos on the right show examples of the natural vegetation in the study area: natural grassland (top) and forest (bottom).

The Chaco has high levels of biodiversity and is home to many endangered and endemic species. The region harbours about 500 species of birds, 150 species of mammals, 120 species of reptiles and 100 species of amphibians (Bucher & Huszar 1999; TNC *et al.* 2005).

Within the mammalian group, the Chaco harbours a number of emblematic and endemic species (10% of the mammal species are endemic). For example, all three species of peccaries are present in the region: the collared peccary (*Pecari tajacu*) (Figure I-4), the white-lipped peccary (*Tayassu pecari*) and the Chacoan peccary (*Catagonus wagneri*). Armadillos are also well represented with 10 species. Among them, the Chaco holds the largest species of armadillo, the giant armadillo (*Priodontes maximus*). In addition, two species of anteaters can be found in the area; the giant anteater (*Myrmecophaga tridactyla)* (Figure I-4) and the Southern Tamandua *(Tamandua tetradactyla)*. The region also harbours the largest terrestrial mammal of South America, the South American tapir (*Tapirus terrestris*) (Figure I-4), which can reach about 310 kg (Canevari & Vaccaro 2007). Finally, among the top predators, jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Figure I-4) are present in the Chaco. Regarding the avian community, only one endemic species is present in the region, the Quebracho Crested Tinamou (*Eudromia formosa*) (Short 1975). Despite the high biodiversity that the Chaco hosts, only 9.1% of the area is protected, with this area representing only 9% of the total distribution of endemic species (Nori *et al.* 2016).

Figure I-4: Examples of mammal species captured by the camera-traps in the study area. A: collared peccary; B: giant anteater; C: South American tapir; D: puma.

The Chaco region has a dynamic land-use history. Grasslands and savannas originally dominated the region, however the natural vegetation was increasingly substituted by woody plants with the arrival of the colonists. This was mainly due to the introduction of cattle ranching, which led to overgrazing and subsequent invasion of the open areas by woody vegetation (Morello & Toledo 1959; Bucher & Huszar 1999). Forest exploitation began in the 1880's, with the demand for forest products such as wood for railway sleepers, fence posts, charcoal and firewood, as well as tannin and oils extracted from trees (Morello, Pengue & Rodríguez 2005; Torrella & Adámoli 2005). Landscape transformation was further boosted by the development of trails and roads, and the expansion of the railway network. However, it was not until the 1990's that the region became a global deforestation hotspot as a result of agricultural expansion, largely in the form of soybean production for livestock feed and industrial cattle ranching (Grau, Gasparri & Aide 2005; Gasparri, Grau & Angonese 2013; Baumann *et al.* 2017). Especially after 2000, deforestation rates in the Chaco soared due to technological advances in agriculture such as the use of new machinery and agrochemicals, and the introduction of genetically modified soybean (Morello, Pengue & Rodríguez 2005; Zak *et al.* 2008; Goldfarb & Zoomers 2013; Baumann *et al.* 2017). This rapid and widespread landscape transformation in the Chaco has had substantial consequences on biodiversity, especially in the Argentine Chaco which has been highly affected by agricultural expansion (Periago *et al.* 2017). As a result, populations of numerous species have drastically declined or suffered local extinctions (Torres *et al.* 2014; Periago *et al.* 2017). For instance, jaguars' range in the Chaco has been reduced significantly over the last two decades (Altrichter, Boaglio & Perovic 2006; Romero-Muñoz *et al.* 2019). Land-use change seems to have affected peccary populations as well, especially the white-lipped and the Chacoan peccary, which currently occur at low densities in the northern part of the Argentine Chaco (Altrichter & Boaglio 2004; Altrichter *et al.* 2012). Beyond the intrinsic values that such emblematic species may have, numerous species in the Chaco are important for ecosystem functioning (Lacher *et al.* 2019). For instance, apex predators such as jaguars and pumas can alter communities' structure, as they regulate the abundance of their herbivorous prey (Ripple & Beschta 2006). Other species, such as the collared peccary and the Pampas fox, play an important role as seed dispersers (Periago *et al.* 2017). Finally, birds also play an important role in regulating ecosystems, by dispersing seeds (e.g., frugivorous species; Blendinger *et al.* (2012)) or physically modifying the environment (e.g., woodpeckers; Cockle, Martin and Wesołowski (2011)). Approaches to detect the effects of

land-use change on biodiversity in the Chaco at an early stage are therefore urgently needed to avoid further defaunation and its widespread cascading effects.

6 The study area: The northern Argentine Dry Chaco

The northern Argentine Dry Chaco was selected as the study area due to its unique spatial configuration of both recently deforested land and intact patches of native vegetation (Figure I-3). Argentina contains the largest proportion of the Chaco ecoregion (60%) and it has experienced high rates of forest loss during the last decades. For instance, 20% of the forest in the Argentine Chaco has been lost between 1985 and 2013 (Baumann *et al.* 2017). While cattle ranching has been the dominant driver of deforestation in the Paraguayan Chaco (Caldas *et al.* 2015), forests in Argentina have mostly been converted to agricultural fields (Zak *et al.* 2008). Much of the Argentine Dry Chaco is suitable for a range of crop types (e.g., soybean, maize, wheat or sorghum), however, soybean is the most important crop in the area (Grau, Aide & Gasparri 2005; Zak *et al.* 2008). Increasing precipitation, technological improvement, as well as increasing soybean prices and yields have been highly beneficial to the cultivation of soybean, and has boosted the expansion of agricultural frontiers in the Argentine Dry Chaco (Grau, Gasparri & Aide 2005; Zak *et al.* 2008). This agricultural expansion has gone paired with high rates of deforestation (Grau, Aide & Gasparri 2005; Grau, Gasparri & Aide 2005), and currently, seven active deforestation frontiers can be identified in the study area (Le Polain de Waroux *et al.* 2018). However, agricultural expansion has not taken place concurrently throughout the region, and thus, the study area provides a unique case for studying the effects of past and recent deforestation on biodiversity.

Although the Argentine Dry Chaco has experienced substantial forest loss during recent decades, the area also contains ample and well-preserved forest patches, particularly in the northeastern part. The study area comprises several protected areas, encompassing a total area of about 870,000 hectares. Among these protected areas, two have been recognized as National Parks (Figure I-3). Copo National Park, located in the centre of the study area, covers an area of about 118,000 ha and was established in 2000. The Impenetrable National Park is the largest protected area in the Dry Chaco at about 130,000 ha. The Impenetrable National Park was founded in 2014 and is in the northeastern part of the study area. For these reasons, the northern Argentine Dry Chaco provides an excellent scenario to study the effects of land-use change on biodiversity, as it contains landscapes that have been transformed

substantially and gradually over time, but also continuous and intact forested areas. Furthermore, by focussing on the Dry Chaco, biodiversity patterns can be compared across space, as climatic conditions are relatively constant across the entire study area. Finally, the Argentine Chaco represents the southernmost part of the geographical range of several species (e.g., Chacoan peccary, giant anteater or South American tapir), underpinning the need for conserving those species and their habitats before their ranges contract further north.

7 Research questions and objectives

The two overarching goals of this thesis were to (I) provide a better understanding of the individual and relative effects of past and contemporary land use on biodiversity in the Argentine Dry Chaco, and (II) develop approaches that capture the impacts of land-use change on biodiversity before local extinctions occur. To achieve these goals, this thesis is subdivided into four main sections related to four core research questions.

Research Question I: Is there evidence of an extinction debt for bird and mammal communities?

Assessment of biodiversity loss due to land-use change has often focussed on relating species distributions to landscape patterns (Mazerolle & Villard 1999; Elith & Leathwick 2009). This approach, however, does not account for changes in the landscape as it only considers a single point in time. Most importantly, it ignores the fact that past landscape patterns may influence contemporary biodiversity, an thus, that there may be a delay between landscape transformation and species extinction.

In Chapter II, I used past and contemporary land-use data to understand the relationship between (1) contemporary biodiversity patterns and (2) contemporary and past landscape patterns. This approach allows for the identification of time-delayed responses to land-use change and its potential extinction debt. In addition, I created a new approach to quantify and map extinction debt. I analysed biodiversity patterns at the community level by using species richness of birds and mammals.

The main objectives related to *Research Question I* were to:

Objective 1.1: Identify time-delayed responses to land-use change of bird and mammal communities.

Objective 1.2: Quantify and map extinction debt across the study area for both taxa.

Quantifying and mapping extinction debt caused by time-delayed responses to land-use change is crucial to counteract future biodiversity loss. Moreover, understanding the differences in the duration of these delayed responses for habitat loss vs. habitat fragmentation is necessary for effective landscape management, leading to the second research question.

Research Question II: What are the time-delayed effects of habitat loss vs. habitat fragmentation on biodiversity?

Accumulating evidence has shown that habitat loss negatively affects biodiversity (e.g., Bender, Contreras and Fahrig (1998), Flather and Bevers (2002), Fahrig (2013)). However, the effects of habitat fragmentation on biodiversity remains unclear (Miller-Rushing *et al.* 2019). Understanding how habitat fragmentation affects biodiversity is challenging, as several factors tend to obscure the effects of fragmentation, such as its long-term effects (Ewers & Didham 2006). While time-delayed responses to habitat loss has received increasing attention (Kuussaari *et al.* 2009; Lira, de Souza Leite & Metzger 2019), it remains unclear how fast biodiversity responds to habitat fragmentation, and whether the time for a community to reach a new equilibrium after landscape transformation is the same after habitat loss as after habitat fragmentation.

In Chapter III, I contributed to bridge this knowledge gap by investigating time-delayed responses of bird and mammal communities to both habitat loss and habitat fragmentation. To do this, I created landscape metrics reflecting habitat amount and habitat fragmentation for the time when biodiversity was sampled, and for the 24 years prior to sampling. Then, I investigated the relationship between (1) contemporary community occupancy and (2) the derived landscape indices at different points in time. This approach provides a nuanced understanding of the time-delayed effects of habitat loss and habitat fragmentation on biodiversity, and it contributes to explaining the diverging findings of habitat loss vs. fragmentation studies.

The main objectives related to *Research Question II* were to:

> Objective 2.1: Test for time-delayed responses to habitat loss and fragmentation by using a detailed database of annual landscape metrics and multi-species occupancy models.
>
> Objective 2.2: Investigate the differences in time delay to extinction between responses to habitat loss vs. habitat fragmentation.

Because species often respond to land-use change with a time delay, population declines can persist over a long time before species go extinct. This leads to the third research question.

Research Question III: What are the direct vs. indirect effects of land-use change on species' populations?

Identifying population declines is crucial for conservation because it enables the identification of populations at risk, and thus provides an opportunity to avoid local extinctions. However, conservation research has often focussed on species extinctions when assessing biodiversity loss rather than population declines (Ceballos & Ehrlich 2002; Ceballos, Ehrlich & Dirzo 2017). Perhaps more importantly, relatively few studies have attempted to distinguish between direct and indirect effects of land use on species' populations (Gibson *et al.* 2011a; Raiter *et al.* 2014; Barlow *et al.* 2016).

In Chapter IV, I addressed the third research question by using (i) contemporary camera-trap data, (ii) past and contemporary land-use data and (iii) occupancy models to estimate changes in species abundance over time. Estimating abundance over time makes it possible to identify areas where populations are already declining, and areas where populations are stable or increasing. By comparing the area in which occupancy decreased with the area affected by agricultural expansion, I isolated direct from indirect effects of land-use change. I tested the utility of this approach by using the threatened giant anteater as an example.

The main objectives related to *Research Question III* were to:

Objective 3.1: Map giant anteater occupancy over time.

Objective 3.2: Assess the relative importance of direct vs. indirect land-use effects on populations.

While identifying population declines can provide an early warning sign for populations at risk, this approach can only detect the negative effects of land-use once the population has begun to decline. Assessing the impacts of land-use change at the individual level can identify populations at risk at an even earlier stage, i.e., before populations start to decline. This leads to the fourth research question.

Research Question IV: How does past and recent deforestation affect species at the population and individual level?

The impacts of deforestation are first noticeable at the individual level (Ellis, McWhorter & Maron 2012). Therefore, it is crucial to focus on processes at the level of individuals, which may forecast future population declines. Conservation physiology focusses on evaluating the

responses of individuals to environmental disturbances such as deforestation by quantifying stress in animals (Dantzer *et al.* 2014). Most previous studies that addressed the effects of habitat loss by employing indices of physiological stress mainly used space-for-time-substitution, thus assessing habitat availability and quality (e.g., (Martínez-Mota *et al.* 2007); Balestri *et al.* (2014); Vynne, Booth and Wasser (2014)), rather than habitat loss. Few studies have simultaneously investigated the effects of habitat loss at both the population and individual level.

In Chapter V, I combined occupancy models and indices of physiological stress to evaluate the impacts of deforestation and associated threats on collared peccaries at the population and individual level. As indices of physiological stress, I employed fecal glucocorticoid metabolites.

The main objective related to *Research Question IV* was to:

> Objective 4.1: Assess the impacts of deforestation and associated threats on collared peccaries at the population and individual level.

In sum, a better understanding of the effects of land-use change on biodiversity is needed, especially in highly dynamic landscapes. Even more importantly, it is essential that these effects are identified before extinctions occurs in order to prevent future biodiversity loss. This can be achieved by investigating the effects of past and contemporary land-use change across multiple levels of organization.

8 Structure of this thesis

This thesis consists of six chapters: the introduction (Chapter I), followed by four core research chapters (Chapter II-V) that relate to the objectives and research questions described above, and a synthesis (Chapter VI) that summarizes the results from the four preceding chapters, and discusses directions for future research and potential implications for conservation management. I wrote the four research chapters as stand-alone manuscripts, which were either published in or submitted to international peer-reviewed journals. Since each research chapter needed to meet the required structure for journal articles (i.e., introduction, material and methods, results and discussion), a thematic overlap between chapters must be accounted for.

Chapter II ***Semper-Pascual, A.**, Macchi, L., Sabatini, F.M., Decarre, J., Baumann, M., Blendinger, P.G., Gómez-Valencia, B., Mastrangelo, M.E. & Kuemmerle, T. (2018). Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. Journal of Applied Ecology, 55, 1218-1229.*

Chapter III ***Semper-Pascual, A.**, Burton, C., Baumann, M., Decarre, J., Gavier-Pizarro, G.I., Gómez-Valencia, B., Macchi, L., Mastrangelo, Pötzschner, F., M.E., Zelaya P.V. & Kuemmerle, T. (in review). How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change?*

Chapter IV ***Semper-Pascual, A.**, Decarre, J., Baumann, M., Camino, M., Di Blanco, Y., Gómez-Valencia, B., & Kuemmerle, T. (2020). Using occupancy models to assess direct and indirect impacts of land-use change on species' populations. Biodiversity and Conservation, 29, 3669-3688.*

Chapter V ***Semper-Pascual, A.**, Decarre, J., Baumann, M., Busso, J.M., Camino, M., Gómez-Valencia, B. & Kuemmerle, T. (2019) Biodiversity loss in deforestation frontiers: Linking occupancy modelling and physiological stress indicators to understand local extinctions. Biological Conservation, 236, 281-288.*

Chapter II:

Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco

Journal of Applied Ecology, 2018, Volume 55, Pages 1218-1229

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Abstract

1. Habitat loss is the primary cause of local extinctions. Yet, there is considerable uncertainty regarding how fast species respond to habitat loss, and how time-delayed responses vary in space.

2. We focused on the Argentine Dry Chaco (ca. 32 million ha), a global deforestation hotspot, and tested for time-delayed response of bird and mammal communities to landscape transformation. We quantified the magnitude of extinction debt by modelling contemporary species richness as a function of either contemporary or past (2000 and 1985) landscape patterns. We then used these models to map communities' extinction debt.

3. We found strong evidence for an extinction debt: landscape structure from 2000 explained contemporary species richness of birds and mammals better than contemporary and 1985 landscapes. This suggests time-delayed responses between 10 and 25 years. Extinction debt was especially strong for forest specialists.

4. Projecting our models across the Chaco highlighted areas where future local extinctions due to unpaid extinction debt are likely. Areas recently converted to agriculture had highest extinction debt, regardless of the post-conversion land use. Few local extinctions were predicted in areas with remaining larger forest patches.

5. *Synthesis and applications*. The evidence for an unpaid extinction debt in the Argentine Dry Chaco provides a substantial window of opportunity for averting local biodiversity losses. However, this window may close rapidly if conservation activities such as habitat restoration are not implemented swiftly. Our extinction debt maps highlights areas where such conservation activities should be implemented.

1 Introduction

Populations of numerous species have recently undergone rapid decline, leading to local extinctions (Pimm *et al.* 2014; Ceballos *et al.* 2015). The primary cause of these declines has been land-use change, mainly through the loss, degradation and fragmentation of habitat (Foley *et al.* 2005; Ehrlich & Pringle 2008). Therefore, understanding how habitat transformation affects local extinctions is crucial to understand ongoing community changes and prevent future biodiversity loss.

Although local extinction can occur immediately, time delays between habitat transformations and biodiversity declines occur frequently (Kuussaari *et al.* 2009; Essl *et al.* 2015). Tilman *et al.* (1994) introduced the term "extinction debt" to describe such time-delayed responses, defined as the number or proportion of extant species predicted to go extinct due to past landscape transformation. Extinction debt can be detected by comparing the relationship between landscape structure and current species richness. Evidence for an extinction debt exists when past landscape structure explains current richness better than current landscape structure. A critical assumption behind this approach is that species richness was in equilibrium before landscape transformation, and species will slowly disappear until the community reaches a new equilibrium with the environment.

The probability and duration of time-delayed responses may vary due to different factors (Ovaskainen & Hanski 2002; Kuussaari *et al.* 2009). First, the magnitude of habitat perturbation may influence the pace with which species respond to landscape transformation (Lira *et al.*, 2012; e.g., species may survive longer if forests are only thinned compared to clear cut). Second, the extent of habitat transformation may influence the number of predicted extinctions (Lawton, May and Raup (1995); e.g., if habitat loss occurs only locally, species may move to remaining patches and therefore persist longer). Finally, species' traits may influence time-delayed responses (Metzger *et al*., 2009; e.g., long-lived species and habitat specialists are more likely to show delayed responses compared to short-lived species and generalists). Given this variability in the probability and duration of time-delayed responses, it is essential to understand the processes underlying such delays. In addition, understanding time-delayed responses is crucial from a conservation perspective, as documenting the number of species found in situ without considering extinction debt might lead to an underestimation of threat level (Hanski & Ovaskainen 2002). Most importantly, identifying extinction debt may provide a window of opportunity for conservation to prevent extinctions (e.g., by restoring habitat for species affected by extinction debt).

Even though time-delayed responses to habitat transformation have received considerable attention, many gaps in our understanding of extinction debt remain. For example, whereas extinction debt should be more likely to occur in landscapes undergoing recent and widespread habitat transformations (Hanski & Ovaskainen 2002), such as in tropical deforestation frontiers, most studies so far have focused on regions where habitat transformation occurred slowly and gradually (Lindborg & Eriksson 2004; Helm, Hanski & Pärtel 2006; Krauss *et al.* 2010; Herrault *et al.* 2016). Most extinction debt studies so far have also focused on relatively small areas (Chen & Peng 2017), and therefore, extinction debt at landscape-to-regional scales, where most conservation planning takes place, is weakly understood. Additionally, there has been a strong focus on plants (Lindborg & Eriksson 2004; Helm, Hanski & Pärtel 2006) and birds (Brooks, Pimm & Oyugi 1999; Metzger *et al.* 2009; Lira *et al.* 2012), while the importance of extinction debt for other threatened taxa (IUCN 2019), especially mammals, remains largely unknown.

While identifying extinction debt provides an imperative to act, many extinction debt studies are non-spatial and thus leave the question of where to act unanswered. Very few studies have attempted to map extinction debt (Cowlishaw 1999; Wearn, Reuman & Ewers 2012; Soga & Koike 2013; Chen & Peng 2017), mostly relying on species–area relationships which are prone to overestimating extinction rates (He & Hubbell 2011). Here, we present a new approach for mapping extinction debt based on mapping species richness in the current landscape and in a new, future equilibrium after relaxation. Our overall goal was to investigate time-delayed responses in bird and mammal communities caused by landscape transformation in the Argentine Dry Chaco, a highly dynamic deforestation frontier. To test for and map extinction debt, we examined the influence of landscape structure on contemporary species richness (2009-2015) based on landscape structure from three time periods (1985, 2000 and contemporary). Specifically, we explored the following research questions:

1. What are the relationships between contemporary richness of birds and mammals, and historical and contemporary landscape structure?
2. Are there differences in time-delayed responses to landscape transformation between birds and mammals, and between forest-dependent species and the entire community?

3. Which areas of the Argentine Dry Chaco are likely to experience local extinctions due to an unpaid extinction debt, and how does the magnitude of this extinction debt vary across space?

2 Material and methods

2.1 Study area

Our study area (Figure II-1) is located in the Gran Chaco region, South America's largest tropical dry forest, stretching into Argentina, Paraguay, Bolivia and Brazil (Bucher & Huszar 1999). Since the 1990s, and especially after 2000, the region experienced one of the highest deforestation rates world-wide, mainly due to the expansion of soybean production and industrial cattle ranching (Grau, Gasparri & Aide 2005; Gasparri & Baldi 2013; Baumann *et al.* 2017). The Chaco is also considered a biodiversity hotspot, harbouring more than 500 birds, 150 mammals, 120 reptiles and 100 amphibian species (TNC *et al.* 2005). Given the high biodiversity, the high anthropogenic pressure and the limited extent of protected areas (9%; Nori *et al. 2016)*, the Chaco is in urgent need of conservation action (Kuemmerle *et al.* 2017).

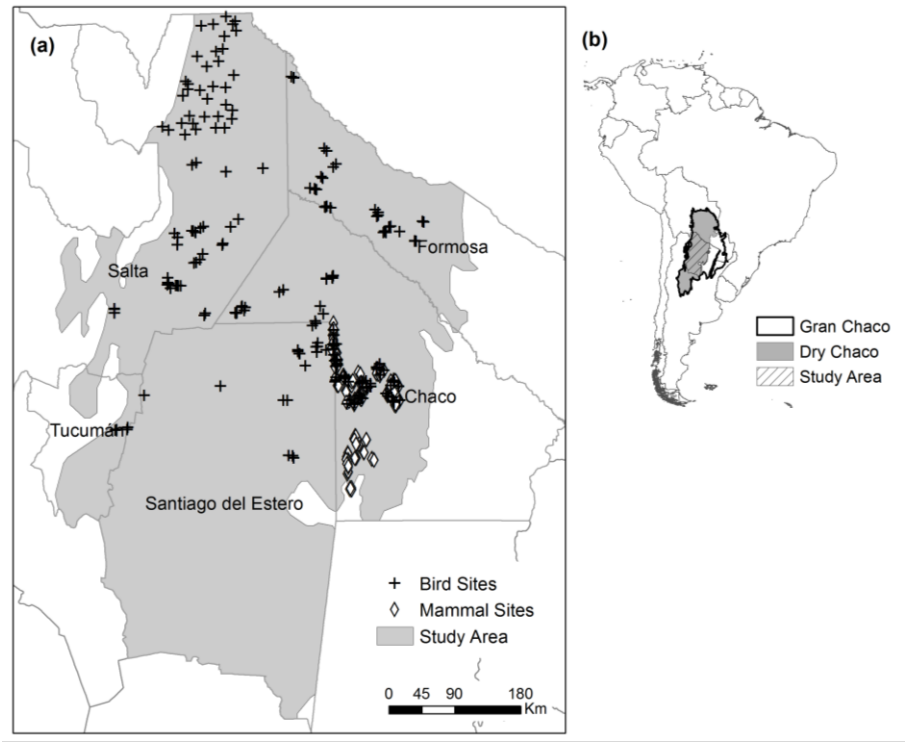

Figure II-1: Location of the study area in (a) Northern Argentina, including bird and mammal sampling sites, and (b) South America

The Chaco can be subdivided along a precipitation gradient, with the Wet Chaco in the East (900–1200 mm), the Dry Chaco in the West (450–700 mm) and a transition area in between (700–900 mm; Cabrera & Willink 1973). We focused on the northern Argentine Dry Chaco (covering c. 32 million ha, Figure II-1), an area characterized by semi-deciduous xerophytic forests, with interspersed shrublands, savannas and grasslands (Cabrera & Willink 1973; Bucher & Huszar 1999). Much of the area has recently been converted to pastures and croplands (Baumann *et al.* 2017), and most remaining natural forests and grasslands are grazed by livestock (Bucher & Huszar 1999).

2.2 Biodiversity data

We used extensive field data available from previous studies on birds (Mastrangelo & Gavin 2012; Macchi *et al.* 2013; Decarre 2015) and mammals (Decarre 2015; Gómez-Valencia 2017). For both taxa, we used (1) total species richness and (2) forest-dependent species richness as our response variables.

Birds were surveyed at 227 sites between 2009 and 2013. Each site was sampled using point counts, where all bird individuals were identified to species level. All species recorded were classified into forest-dependent (hereafter: forest species) and species preferring non-forest environments (hereafter: non-forest species) according to our own field experience (Macchi *et al.* 2013; Decarre 2015), experts' knowledge (Torres *et al.* 2014) and existing literature (Ridgely & Tudor 1994b) (Table SI II-1). We excluded migratory species to minimize seasonal effects.

In total, we included 212 bird species in our analyses of which 74 were forest species (Table SI II-1). Because the number of point counts per site varied depending on the study (4, 6 and 9 point counts), we calculated rarefied richness for the entire community and for the forest species using sample-based rarefaction curves to correct for uneven sampling efforts. We rarefied all sites to the smallest sampling effort (i.e., 4 point counts) using the *vegan* package in R (Oksanen *et al.* 2016). A sample coverage curve (Figure SI II-1) suggests that rarefying to 4 point counts does only marginally underestimate species richness as opposed to rarefying and extrapolating to 6 or 9 point counts, a conclusion also supported by the relationship between original richness and estimated rarefied richness (Figure SI II-2).

Medium and large-bodied mammals were surveyed at 226 sites from 2012 to 2015, using camera traps. Sites were chosen randomly, while avoiding trails. Mammals were classified into forest and non-forest species following expert recommendations (Decarre 2015; Gómez-Valencia 2017) and literature (Canevari & Vaccaro 2007). We documented a total of

26 mammal species in the study area, with 11 forest species (Table SI II-2). Cameras were active between 9 and 153 camera-trap nights per site (M = 43), with 9719 camera-trap nights in total. To correct for differences in camera-trap nights among sites without having to discard substantial amounts of data, we generated rarefaction curves following Colwell *et al.* (2012), using the R package *iNEXT* (Hsieh, Ma & Chao 2016). Instead of rarefying all the sites to the lowest sampling effort, this method allows to rarefy sites with a high number of camera-trap nights and extrapolate sites with a low number of camera-trap nights to a common number (i.e., in our case 39 and 40 camera-trap nights for the entire community and for the forest species respectively, which represents the mean number of camera-trap nights, after excluding the outliers). Since *iNEXT* cannot handle sites with identical capture records, we excluded duplicate sites yielding a final sample size of 223 sites for the entire community and 225 for forest species.

Further details on the field methods are provided in Text SI II-1, including a comparison of original and the estimated rarefied richness (Figure SI II-2).

2.3 Landscape variables

We selected two landscape predictors as proxies for habitat availability (percentage of forest, percentage of core forest) and three landscape predictors as proxies for habitat connectivity (percentage of edge between forest and non-forest patches, percentage of connectivity, aggregation index) around each sampling site (Table II-1: and Table SI II-3). We estimated these five landscape predictors for each time period, i.e., 1985, 2000 and contemporary (Table II-1:), based on different Landsat-based land-cover data. We used the Global Forest Change map from (Hansen *et al.* 2013) to derive contemporary (from 2009 to 2013) and past (2000) forest extent and configuration, and a land-cover map from Baumann *et al.* (2017) to assess past (1985) landscape configuration (Text SI II-2). Both maps have a high accuracy (99% and 88%, respectively) and comparing the estimated forest loss areas for the post-2000 period suggests that both maps are well-aligned. Since bird data were collected in different years (from 2009 to 2013), we extracted contemporary landscape data for the specific year in which a site was sampled, thus accounting for land-use change during the sampling period (e.g., sites sampled in 2009 were related to forest cover from 2009). For the mammal dataset (sampled between 2012 and 2015), we used forest maps from 2013 since more recent land-cover maps were not available.

Table II-1: Predictors for explaining bird and mammal richness in the Chaco.

Predictor by group	**Name**	**Description**
Landscape structure		
Extent of forest	Forest	Percentage of forest in the buffer
Extent of core forest	Core	Percentage of interior area of forest excluding forest perimeter in the buffer
Extent of edge between forested and non-forested patches	Edge	Percentage of outside perimeter pixels in the buffer
Extent of connectivity	Connec	Percentage of pixels connecting different forest patches in the buffer
Aggregation	Aggre	Number of like adjacencies between forest patches, divided by the maximum possible number of like adjacencies between forest patches, multiplied by 100 (to convert to a percentage) (McGarigal 2014)
Human Disturbance		
Distance to big settlements	DistTown	Euclidean distance (km) to the closest settlement with more than 900 inhabitants
Distance to *puestos*	DistPuesto	Euclidean distance (km) to the closest *puesto*
Distance to paved roads	DistRoad	Euclidean distance (km) to the closest paved road
Density of non-paved roads	DensRoad	Density of non-paved roads in the buffer (km/km^2)
Climate		
Long-term temperature	Temp	Mean temperature (°C) for the 10 years before each period of time (1975-1985 for 1985; 1990-2000 for 2000; and 2000-2010 for the contemporary period)
Long-term precipitation	Prec	Mean precipitation (mm) for the 10 years before each period of time
Aridity	Aridity	Aridity index for the year when the species were sampled
Water availability		
Density of rivers	DensRiver	Density of rivers in the buffer (km/km^2)
Distance to water bodies	DistWater	Euclidean distance (km) to the closest permanent water body

We derived landscape data in a circular buffer around each sampling site. For birds, we used a 3-km radius in accordance with other studies testing the influence of landscape configuration on bird richness and abundance (Mitchell, Lancia & Gerwin 2001; Deconchat, Brockerhoff & Barbaro 2009; Mastrangelo & Gavin 2014). For mammals, we used a 2-km radius, which represents the average home range sizes of medium and large mammals found in the area (Beisiegel & Mantovani 2006; Canevari & Vaccaro 2007; Kasper, Soares & Freitas 2012; Schai-Braun & Hackländer 2014; IUCN 2019). We used Morphological Spatial Pattern Analysis (Vogt *et al.* 2007), available in the GUIDOS software, and *SDMTools* package (VanDerWal *et al.* 2014) in R to derive landscape metrics. To investigate whether extinction debt is caused by landscape transformation or other factors, we also included a number of control variables related to human disturbance, climate and water availability that could affect birds and mammals in the Dry Chaco (Table II-1: and Table SI II-3).

2.4 Testing for extinction debt

Investigating extinction debt relies on the assumption that communities were in equilibrium with the landscape before major habitat perturbations occurred (Kuussaari *et al.* 2009). Although degradation in the Dry Chaco started long ago, major changes in the landscape have only occurred since the mid-1990s (Caldas *et al.* 2015; Baumann *et al.* 2017). We therefore assumed an equilibrium state at the beginning of our study period. We carried out two analyses: first, we tested for the existence of extinction debt separately for birds and mammals. Second, we mapped the magnitude of the potential extinction debt per group. To test for the existence of an extinction debt, we first investigated the relationships between contemporary species richness and (1) contemporary landscape predictors, (2) year-2000 predictors, and (3) year-1985 predictors (i.e., each model only contained landscape predictors from one time period). For each time period, we considered four response variables: the contemporary rarefied richness of (1) all birds, (2) forest birds, (3) all mammals and (4) forest mammals. For each time period and response variable, we parametrized models with and without landscape variables to investigate whether extinction debt was caused by landscape transformation or other factors (e.g., climate change; Table SI II-4 and Table SI II-5). When two predictors were collinear (Spearman correlation coefficient >0.6), we retained the variable with the most ecologically meaningful relationship with species richness (Table SI II-4 and Table SI II-5). We standardized all predictors (M = 0, SD = 1) to assess their relative importance (Schielzeth 2010). Since bird data were from different sources, we controlled for varying sampling designs using linear mixed models that included the categorical variable sampling design as a random intercept, using the R package *nlme* (Pinheiro *et al.* 2016). For the mammal data, we used simple linear models, as the study design did not vary between the two datasets.

When analysing forest species, for both birds and mammals, we used a two-step hurdle modelling approach to account for the zero-inflation caused by many sites without forest species. We first modelled the probability of forest species occurrence (presence–absence data), and then analysed the variation in the number of forest species for sites with forest species (presence-only data). We fitted our data using generalized linear models (generalized linear mixed models for the forest birds) with a binomial distribution for the presence–absence model, and a gamma distribution for the presence-only model using the R package *lme4* (Bates *et al.* 2015). Finally, we checked for the existence of spatial autocorrelation by computing the semi-variogram of the residuals. We used the Akaike's information criterion (AIC; Burnham & Anderson 2002) to determine which model explained species richness

best, ranked models using ΔAIC, considering models with a ΔAIC <2 to equally be supported. We also calculated Akaike weights to quantify the probability of each candidate model of being the best model (Wagenmakers & Farrell 2004). For the hurdle models, we calculated AIC by adding the AICs of the two individual models (Zuur & Ieno 2016).

2.5 Mapping extinction debt

To map extinction debt for the entire community, we used our models to predict (1) contemporary total species richness and (2) total species richness after extinction debt has been paid (Figure II-2). This assumes that communities are in equilibrium before large-scale habitat transformation (before 1990 in our case). Following land-use change, species are lost either immediately or gradually, due to extinction debt, until a new, future equilibrium is reached. The difference between the old and new equilibrium represents the total number of species going extinct as a consequence of land-use change, whereas the difference between contemporary richness and the future equilibrium represents the extinction debt (Figure II-2).

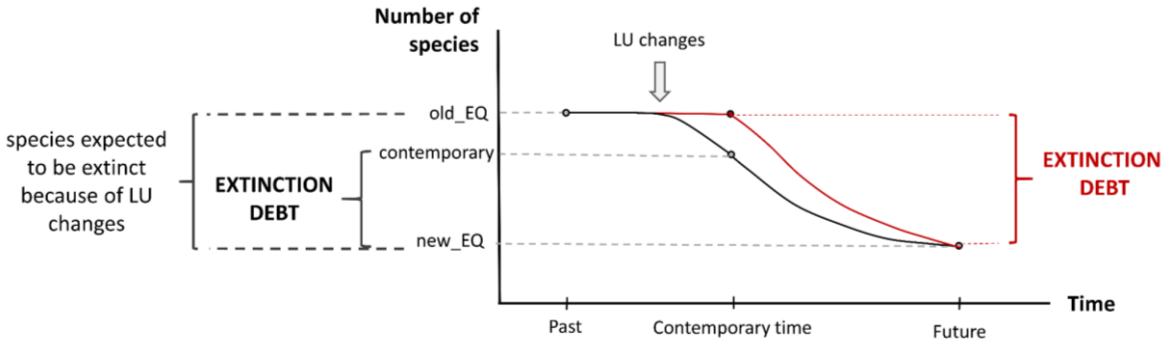

Figure II-2: Species can be lost immediately after land-use change or with a time delay. Extinction debt refers to those species that will go extinct in the future (compared to now). Extinction debt can be lower than the total number of species lost if some species have already gone locally extinct.

To predict contemporary richness patterns, we used the model that explained contemporary biodiversity patterns as observed via bird counts and mammal camera trapping best (i.e., the model with lowest AIC; hereafter: best-fitting model, Figure II-3). In the presence of an extinction debt, this model should contain historical landscape predictors. We then projected the same best-fitting model to contemporary landscape patterns (i.e., using the same set of predictor variables and regression coefficients, but replacing historical landscape predictors with contemporary predictors). This predicts the total number of species that can persist in the new landscape, that is species richness from the past equilibrium minus those species

lost immediately (and therefore not in our dataset) and those that will be lost due to extinction debt. We refer to this as the future equilibrium (note that this does not include the effect of possible future habitat transformation). We then calculate extinction debt as the difference between predicted contemporary and future total richness, with positive differences indicating sites where local extinctions are likely to happen.

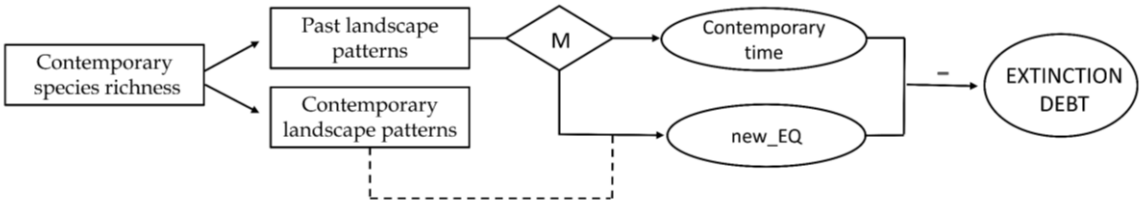

Figure II-3: Approach followed to map extinction debt.The model including past landscape patterns (our best-fitting model, M) was used to predict contemporary species richness. The same model was then projected to contemporary landscape patterns, thus predicting species richness in the new, future equilibrium (new_EQ), once extinction debt has been fully paid (and assuming no further habitat transformation). The difference in the number of species between the contemporary time and the new equilibrium represents the extinction debt.

Since the aim of our study was to investigate extinction debt caused by habitat transformation, we used the best-fitting model using only landscape variables to map extinction debt (landscape structure variables in Table SI II-4 and Table SI II-5). We log-transformed the variable percent of core forest for the mammal dataset to meet the assumption of linearity (we had not log-transformed predictor variables when testing for extinction debt since we wanted to keep models comparable). We developed two maps showing where extinction debt is likely to occur (one for birds and one for mammals) at 300-m resolution, which required us to summarize landscape variables around each pixel using 3-km (birds) or 2-km (mammals) buffers using a circular moving window. To facilitate map interpretation, we distinguished the following classes: high extinction debt (more than 20% of contemporary species richness expected to go extinct because of past landscape transformation) and low extinction debt (5%–20% expected to go extinct). In addition, we identified stable areas (expected increase or decrease less than 5%) and colonization areas (expected increase more than 5%).

3 Results

The contemporary total species richness of both birds and mammals in the Argentine Dry Chaco was better explained by models based on past landscape variables compared to models relying on contemporary landscape variables. Models based on landscape variables from 2000 were consistently selected as best-fitting models (ΔAIC <2, Table II-2:), for both birds and mammals. Models based on landscape predictors from 1985 performed worse than models containing contemporary predictors (Table II-2:). Comparing models with and without landscape variables showed that including landscape variables markedly improved model fitting for the best models (Table II-2:). The regression coefficients of the landscape variables were generally higher than those of other variables (Table II-3:), with the percentage of core forest and connectivity showing the strongest effects. Bird and mammal richness was positively related to core forest, for both the models using 2000 and contemporary landscape data; however, this relationship was stronger in the 2000 model (Table II-3: and Figure II-4). Together, these results suggest that contemporary species richness of the entire communities was more related to past (i.e., year 2000) than contemporary landscape patterns.

Table II-2: AIC, ΔAIC and model weights (AICw) for all candidate models (ranked by AIC).Full models include all predictors, noLS models exclude landscape structure predictors and null models do not include any predictors.

All Species				**Forest Species**			
Model	**AIC**	**ΔAIC**	**AIC_w**	**Model**	**AIC**	**ΔAIC**	**AIC_w**
Birds							
Birds_2000_full	1618.89	0.00	0.76	BirdsFor_2000_full	1248.67	0.00	1.00
Birds_contemp_full	1621.18	2.29	0.24	BirdsFor_contemp_full	1260.31	11.65	0.00
Birds_1985_noLS	1631.66	12.77	0.00	BirdsFor_1985_noLS	1271.83	23.16	0.00
Birds_1985_full	1635.25	16.36	0.00	BirdsFor_1985_full	1273.85	25.19	0.00
Birds_2000_noLS	1637.54	18.65	0.00	BirdsFor_2000_noLS	1277.32	28.65	0.00
Birds_contemp_noLS	1654.61	35.72	0.00	BirdsFor_contemp_noLS	1313.04	64.37	0.00
Birds_null	1684.00	65.10	0.00	BirdsFor_null	1359.73	111.07	0.00
Mammals							
Mam_2000_full	1001.81	0.00	0.78	MamFor_2000_full	503.05	0.00	0.96
Mam_contemp_full	1005.06	3.25	0.15	MamFor_contemp_full	509.36	6.32	0.04
Mam_1985_full	1008.80	6.99	0.02	MamFor_2000_noLS	520.76	17.72	0.00
Mam_1985_noLS	1009.12	7.31	0.02	MamFor_contemp_noLS	523.90	20.85	0.00
Mam_contemp_noLS	1010.20	8.39	0.01	MamFor_1985_full	529.75	26.70	0.00
Mam_null	1011.76	9.95	0.01	MamFor_1985_noLS	532.85	29.80	0.00
Mam_2000_noLS	1014.76	12.95	0.00	MamFor_null	546.09	43.05	0.00

Table II-3: Parameter estimates of the two best models (contemporary and 2000 period in Table II-2:). For the bird models, fixed effects estimates from the linear mixed models are shown. For the mammal models, estimates are derived from linear models. All variables are standardized to 0 mean and 1 standard deviation for comparison.

	Birds				**Mammals**			
	Contemporary		**2000**		**Contemporary**		**2000**	
	Estimate	**95% CI**	**Estimate**	**95% CI**	**Estimate**	**95% CI**	**Estimate**	**95% CI**
Intercept	19.83	22.76,16.91	19.03	22.05,16.01	3.74	4.04,3.45	3.74	4.04,3.45
Core	2.87	4.62,1.13	4.46	6.25,2.66	0.79	1.29,0.29	0.82	1.23,0.41
Edge	1.15	2.69,-0.39	0.75	2.13,-0.64	-0.14	0.25,-0.54	-0.19	0.11,-0.49
Connec	3.30	4.82,1.77	1.88	3.43,0.33	0.18	0.56,-0.21		
DistTowns	-1.02	0.31,-2.34	-1.64	-0.29,-2.98				
DistRoads	0.49	1.85,-0.87	1.79	3.46,0.12	-0.06	0.32,-0.44	0.13	0.52,-0.25
DensRoads	-1.00	0.15,-2.16	-0.70	0.45,-1.85	0.10	0.47,-0.26	0.19	0.61,-0.22
DistPuestos	-0.66	0.68,-2.00	0.41	1.99,-1.16			-0.08	0.45,-0.6
Temp			1.45	3.13,-0.23				
Prec	-0.68	0.99,-2.35	0.68	2.32,-0.97			0.17	0.73,-0.38
Aridity	2.01	3.58,0.44	1.07	3.02,-0.88	-0.32	0.05,-0.69	-0.21	0.36,-0.78
DensRivers	0.68	1.97,-0.61	1.21	2.55,-0.14				
DistWater	1.47	2.93,0.02	1.75	3.29,0.21	-0.33	0.03,-0.70	-0.24	0.18,-0.65

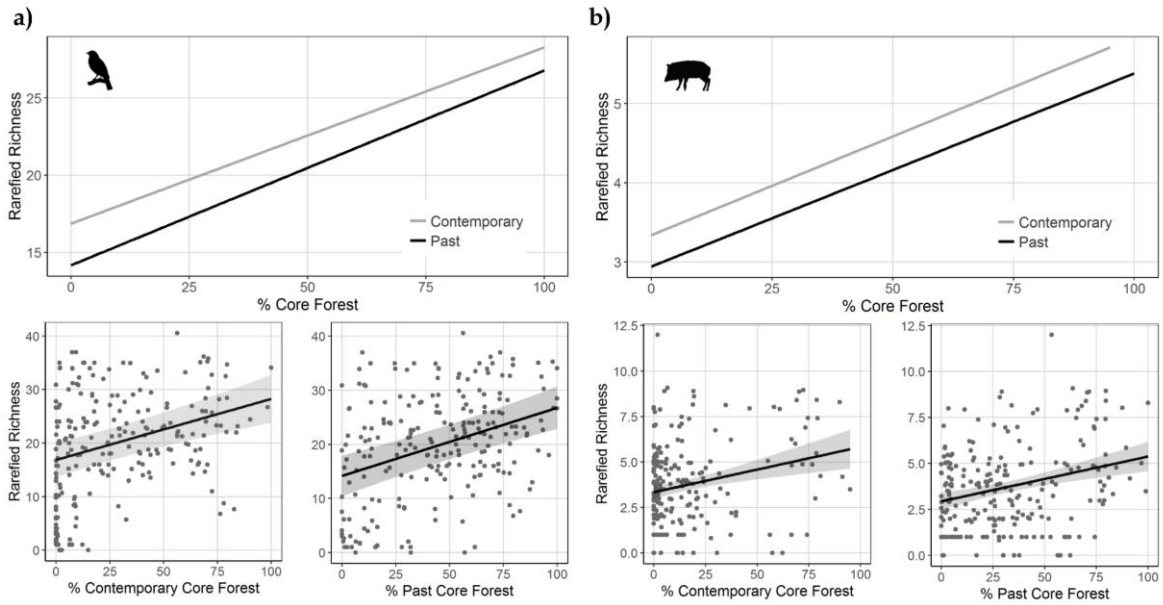

Figure II-4: Correlation between contemporary (a) bird and (b) mammal richness and contemporary and past (2000) percentage of core forest. Upper graphs show regression lines for both contemporary and past core forest. The lower graphs show the linear regression between rarefied richness and percentage of core forest for each period separately (with 95% confidence intervals around regression lines).

Our projections of extinction debt showed that for both birds and mammals, areas recently deforested due to agricultural expansion were most likely to experience future local bird and mammal extinctions (e.g., the Salta-Santiago del Estero border or the Chaco-Santiago del Estero border; Figure II-5). In contrast, few future local extinctions were expected in areas with larger patches of forest such as Copo National Park (North of Santiago del Estero Province) or the Impenetrable (North of Chaco Province). Although the spatial patterns of extinction debt were similar across birds and mammals, the magnitude of the extinction debt was higher for birds. High extinction debt was predicted for a larger area for birds (5% of the study region) than for mammals (0.3% of the study region, Figure II-5 and Figure SI II-3). In addition, high extinction debt for birds was similar in areas converted to crops and pastures (Figure II-6). Low extinction debt, both for birds and for mammals, was more likely to occur in forested areas around agricultural fields (Figure II-5 and Figure II-6).

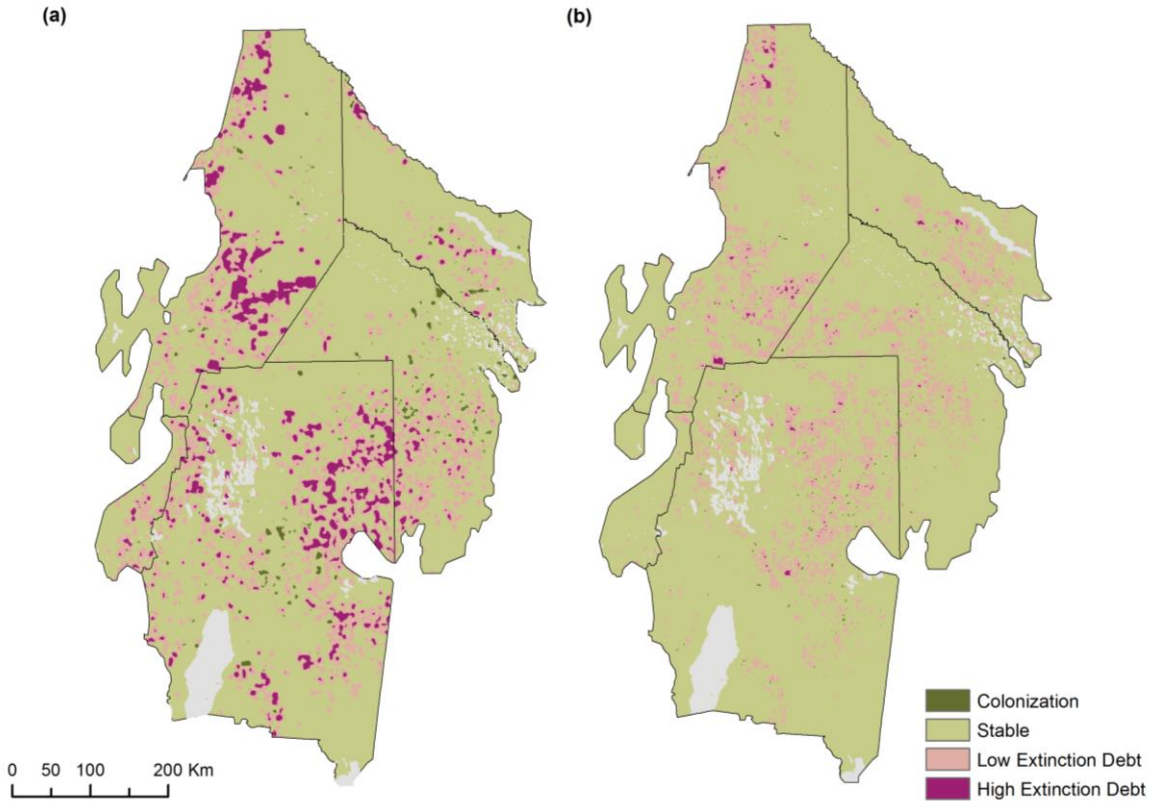

Figure II-5: Extinction debt for (a) birds and (b) mammals in the study region. Permanent water bodies and salt plains are depicted as light grey. Four categories are represented in the map: high extinction debt (future decrease >20% compared to contemporary richness), low extinction debt (future decrease 5%–20%), stable areas (<5% increase or decrease) and colonization areas (>5%).

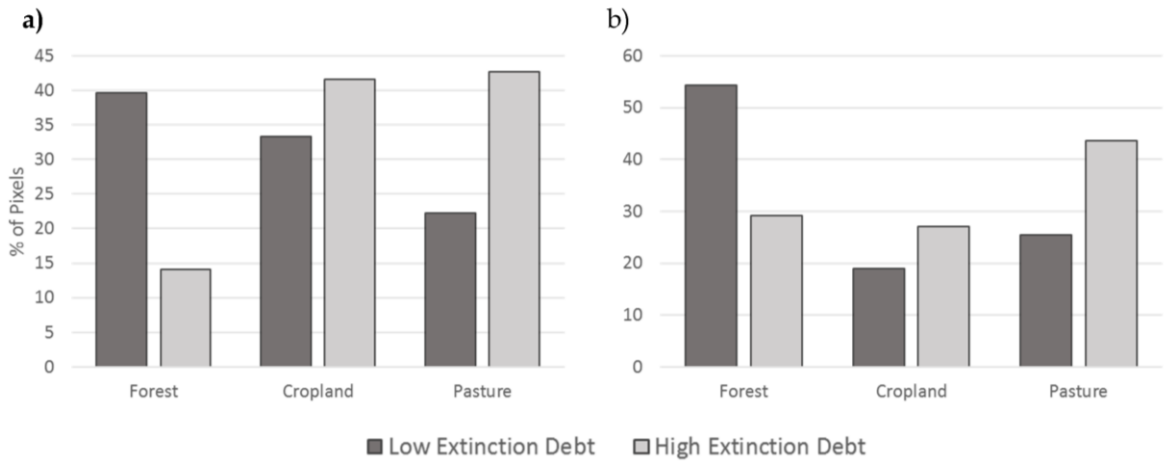

Figure II-6: Percentage of extinction debt pixels located in forest, cropland and pasture pixels for (a) birds and (b) mammals.The graph is the result of the intersection between our extinction debt map and the 2013 land-cover map from Baumann et al. (2017).

4 Discussion

Habitat loss and fragmentation threaten biodiversity globally, and understanding time-delayed responses of communities to habitat transformation might help to counteract future extinctions. We found strong evidence for extinction debt for birds and mammals in the Argentine Dry Chaco, but also that this extinction debt may be paid soon. Interestingly, relaxation time (i.e., the time needed to reach a new, future equilibrium) was similar for birds and mammals (between 10 and 25 years), and for forest specialists and the entire community. Additionally, extinction debt is more likely to occur in areas where agriculture has expanded recently, but its magnitude is comparable across systems with different post-deforestation land use (e.g., ranching vs. cropping). In these areas, up to 56% and 29% of the extant birds and mammals, respectively, may go locally extinct if conservation actions are not implemented soon.

Past landscape structure explained contemporary bird and mammal richness better than contemporary landscape structure, supporting the hypothesis of time-delayed responses to habitat transformation in the Chaco. This seems reasonable given the high rate of habitat transformations in deforestation frontiers (Numata *et al.* 2011; Carlson *et al.* 2013; Baumann *et al.* 2017) and is in line with the few studies that have investigated extinction debt in such highly dynamic landscapes (Metzger *et al.* 2009; Lira *et al.* 2012). Our long-term forest-cover dataset allowed us to provide upper and lower bounds for this time delay: landscape patterns from 2000 explained contemporary richness best, indicating that average relaxation time is greater than 10 years, but contemporary richness was not associated with 1985-

landscape structure, suggesting that relaxation time is less than 25 years. Major landscape transformation in the Chaco landscape began only at the end of the 20th century (Caldas *et al.* 2015; Baumann *et al.* 2017), explaining why bird and mammal communities were likely still in equilibrium in 1985.

The time-delayed response of c. 10–25 years we found is similar to those found in other studies for vertebrates. For example, MacHunter *et al.* (2006) found an evidence of relaxation time for birds of 22 years in southeastern Australia. Similarly, Sales *et al.* (2015) reported a time-delayed response of 11 years for a primate species in Brazil. An exception is the work by Brooks, Pimm and Oyugi (1999), who estimated relaxation times for tropical birds of >50 years using species-area relationships. Such models, however, are prone to overestimate extinction risk and thus extinction debt (He & Hubbell 2011). The relaxation time we found is considerably shorter than that found for plants (Lindborg & Eriksson 2004; Helm, Hanski & Pärtel 2006; Krauss *et al.* 2010) which can exceed a century (Vellend *et al.* 2006).

Extinction debt did not vary substantially among birds and mammals. Species-specific traits, such as longevity, home range size, diet or habitat association, may influence extinction debt, but the evidence remains inconclusive (Kuussaari *et al.* 2009; Hylander & Ehrlén 2013). For example, Metzger *et al.* (2009) found extinction debt for birds in the Atlantic Forest but not for small mammals, while another study from the same region did not find extinction debt for either taxa (Lira *et al.* 2012). Although there is a general lack of information on the longevity of many species we studied, a likely explanation for the similar time delays we found are relatively similar longevity and generation times (e.g., average longevity for Chacoan mammals is around 15 years (Bobick & Peffer 1993), while average longevity for Neotropical birds is around 10 years (Snow & Lill 1974)). Further research is needed to clarify the effect of longevity or other traits on extinction debt. In addition, that both taxa had time-delayed responses to landscape transformation suggests both birds and mammals in the Chaco are equally habitat-dependent.

While we found extinction debt both for forest species and the entire community, support was stronger for forest species. This can be expected and supports the idea that assessing only specialist species may be more effective for detecting extinction debt (Kuussaari *et al.* 2009). On the other hand, reliably classifying species into forest and non-forest specialists is challenging in tropical dry forests and savannas that are characterized by heterogeneous landscapes and ecotones (Murphy & Lugo 1986). The fact that we found extinction debt for

the bird and mammal communities as a whole highlights that even those species not strictly linked to forests may still critically depend on the forest (e.g., anteaters use forest patches to shelter and rest; Quiroga *et al.* 2016). By omitting these species, extinction debt may thus be underestimated.

Our maps of unpaid extinction debt in the Argentine Dry Chaco indicated similar spatial patterns for both birds and mammals, but different magnitudes. Higher extinction debt was predicted in areas where deforestation has been most drastic recently. These areas were mostly classified as having high extinction debt for birds but low extinction debt for mammals, suggesting that although both taxa were affected by extinction debt, that is, a percent of the contemporary number of species will go extinct due to past landscape transformation, this percentage is higher for birds than for mammals. These results are similar to the findings of Wearn, Reuman and Ewers (2012) who also reported higher magnitudes of extinction debt for birds than for mammals. Extinction debt was small in areas still characterized by high forest cover, such as the Copo NP and the Impenetrable NP, or areas unsuitable for intensified agriculture, such as the regularly flooded areas in the north of our study region.

Interestingly, extinction debt for birds did not differ much between post-deforestation land uses (cropland or pastures). This can be explained by the conversion process itself, which is equally drastic for both post-deforestation land uses, since all natural vegetation is removed and exotic grasses are sown when converting to intensified pastures (Baumann *et al.* 2017). Low extinction debt for both birds and mammals, instead, was generally found in forested areas located around crops and pastures, highlighting the importance of the landscape context.

We used an extensive field dataset to quantify and map extinction debt in the Dry Chaco, and our models were very robust. Still, our analyses do not come without uncertainty. First, while we used a large field dataset, additional data covering a larger area would have been useful, especially for mammals. Second, while we have explored extinction debt for both, forest and the entire community, our models for forest species did not allow projecting extinction debt in space. Few approaches exist for zero-inflated datasets (Zuur & Ieno 2016), and our hurdle modelling approach does not allow for predicting in space. Developing statistical methods to better deal with zero-inflated datasets would be useful to overcome such limitations. Third, we conservatively rarefied our bird data to the lowest number of point counts (4), which may underestimate extinction debt. Rerunning all our analyses for

rarefication to 6 and 9 point counts did not change any of our conclusions (Figure SI II-4), but our maps of extinction debt are likely conservative. Finally, we considered land conversions only, whereas forest degradation is also widespread and may play an important role in relation to extinction debt. Including forest degradation, as soon as adequate data become available, as an explanatory variable in models estimating extinction debt will therefore represent an important advancement.

4.1 Synthesis and applications

Several major implications for conservation planning derive from our work. First, our results show that bird and mammal richness in active deforestation frontiers does respond to habitat loss with a time delay and therefore, predicting species richness without considering extinction debt may lead to an overestimation of the contemporary number of species (Figure SI II-5 and Figure SI II-6). This is encouraging as our results also suggest that despite drastic habitat loss, a window of opportunity may often exist for saving species otherwise likely facing extinction. In such cases, conservation planning should not only focus on protecting remaining forests, but also exploring options to restore already transformed areas. However, our results highlight that extinction debt for birds and mammals in the Chaco, some of which are of conservation concern, may be paid relatively quickly. In our case, the time to a new equilibrium state, when extinction debt will have been paid, may be as short as a decade, highlighting the urgency of conservation action if local extinctions are to be averted. Second, extinction debt was highest in areas where agricultural activities are expanding, with small differences regarding post-deforestation land use for birds. This provides a cautionary note regarding the compatibility of cattle ranching with biodiversity conservation, at least in terms of the intensified ranching systems that have expanded in the Chaco since 2000. Finally, many of the world's active agricultural frontiers are located in tropical forests and savannas that harbour high biodiversity (Schiesari *et al.* 2013). Our study shows that considering land-use legacies and time-delayed responses of biodiversity to habitat transformations, especially in highly dynamic landscapes, is critical for effective biodiversity monitoring and conservation planning.

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Supplementary Information

Text SI II-1: Field sampling design for the biodiversity data.

The bird dataset is based on three comparable multi-year studies, conducted between 2009 and 2013 (Mastrangelo & Gavin 2012; Macchi *et al.* 2013; Decarre 2015). All studies relied on point counts established within 227 different sites spread along the study area where birds were recorded by sight or sound within a radius around each point. Bird data from Mastrangelo & Gavin (2012) was recorded in 2010 at 33 sites located in five different habitats: forest, *puestos*, low intensity silvopasture, intermediate intensity silvopasture, and high intensity silvopasture. In each site, 6 points with a 25 m fixed radius were randomly located and birds were recorded during 20 minutes. Macchi *et al.* (2013) surveyed 148 sites between 2009 and 2013. Sites were located in 6 different types of habitats: forest, *puestos*, silvopastures, natural grasslands, pasture plots and soybean plots. Inside each site, nine points were established in a 300 m grid. For each point count, birds were recorded during 10 minutes using a 20 m fixed radius. The bird community in Decarre (2015) dataset was sampled in 2012 at 46 sites located in four different types of habitat: forest, silvopastures, forest strips and agricultural plots. Inside each site, four points were randomly selected. Points were at least 200 m apart and birds were recorded during 10 minutes per point inside a fixed radius of 100 m. Additional, detailed information regarding the field methodology is described in Macchi *et al.* (2013), Mastrangelo & Gavin (2012) and Decarre (2015).

The mammalian community was characterized using data from two extensive camera trap surveys (Decarre 2015; Gómez-Valencia 2017). In both studies, cameras were randomly placed at each site avoiding a trail-based design. Camera traps from the study of (Decarre 2015) were deployed at 130 sites located in 5 different types of habitat: forest, silvopastures, forest strips, agricultural plots and natural grasslands. Camera traps were attached to a tree or a wooden stick at an average height of 30 cm. The mean distance between the nearest camera sites was 1.7 km. Camera traps in Gómez-Valencia (2017) were set at 93 sites within forest fragments with varying forest cover percentages. Cameras were located at a height of 40-45 cm and separated for an average distance of 1.2 km. Further detail about the camera placement and images processing is described in Decarre (2015) and Gómez-Valencia (2017).

Text SI II-2: Generation of forest cover maps from the Global Forest Change dataset.

The Global Forest Change dataset contains tree canopy cover for the year 2000 and forest cover loss from the time period 2000 to 2014. We first generated a forest cover map for the year 2000 defining as forest those pixels with a tree canopy cover >25%, which works well for the Chaco region (Hansen *et al.* 2013). Second, we derived forest cover for the years between 2009 and 2013 by updating this year-2000 forest cover map with the forest cover loss information for each year. For all forest cover maps, we eliminated forest patches smaller than 0.72 hectares (8 pixels) as such small patches are unlikely to provide sufficient habitat for the species in focus in our study.

Table SI II-1: List of bird species recorded in the study area between 2009 and 2013. We defined forest species as following: "Forest-dependent species are species that inhabit areas dominated by trees and that depend on such habitat for key ecological processes (i.e., foraging, shelter and/or breeding). Such species are uncommon or absent in open habitats like savannas, grasslands, wetlands and shrublands". Bird species were categorized into forest and non-forest species according to expert knowledge (Macchi *et al.* 2013; Torres *et al.* 2014; Decarre 2015) and literature (Short 1975; Ridgely & Tudor 1994b; Del Hoyo *et al.* 2014).

Scientific name	English name	Habitat
Accipiter bicolor	Bicolored Hawk	Forest
Agelaioides badius	Greyish Baywing	Non-forest
Agelasticus cyanopus	Unicolored Blackbird	Non-forest
Agelasticus thilius	Yellow-winged Blackbird	Non-forest
Alopochelidon fucata	Tawny-headed Swallow	Non-forest
Amazona aestiva	Turquoise-fronted Amazon	Forest
Ammodramus humeralis	Grassland Sparrow	Non-forest
Anhinga anhinga	Anhinga	Non-forest
Anthus chacoensis	Pampas Pipit	Non-forest
Anthus furcatus	Short-billed Pipit	Non-forest
Anthus lutescens	Yellowish Pipit	Non-forest
Aramides ypecaha	Giant Wood-rail	Non-forest
Aramus guarauna	Limpkin	Non-forest
Ardea alba	Great White Egret	Non-forest
Ardea cocoi	Cocoi Heron	Non-forest
Arremon flavirostris	Saffron-billed Sparrow	Forest
Arundinicola leucocephala	White-headed Marsh-tyrant	Non-forest
Asio clamator	Striped Owl	Non-forest
Asthenes baeri	Short-billed Canastero	Forest
Athene cunicularia	Burrowing Owl	Non-forest
Bubulcus ibis	Cattle Egret	Non-forest
Busarellus nigricollis	Black-collared Hawk	Non-forest
Buteogallus meridionalis	Savanna Hawk	Non-forest
Buteogallus urubitinga	Great Black Hawk	Forest
Cacicus chrysopterus	Golden-winged Cacique	Forest
Cacicus solitarius	Solitary Cacique	Forest
Cairina moschata	Muscovy Duck	Non-forest
Callonetta leucophrys	Ringed Teal	Non-forest
Campephilus leucopogon	Cream-backed Woodpecker	Forest
Camptostoma obsoletum	Southern Beardless Tyrannulet	Forest
Campylorhamphus trochilirostris	Red-billed Scythebill	Forest
Caracara plancus	Southern Caracara	Non-forest
Casiornis rufus	Rufous Casiornis	Forest
Cathartes aura	Turkey Vulture	Non-forest
Cathartes burrovianus	Lesser Yellow-headed Vulture	Non-forest
Chaetura meridionalis	Southern Swift	Non-forest
Chauna torquata	Southern Screamer	Non-forest
Chlorospingus flavopectus	Common Bush-tanager	Forest
Chlorostilbon lucidus	Glittering-bellied Emerald	Non-forest
Chunga burmeisteri	Black-legged Seriema	Forest
Ciconia maguari	Maguari Stork	Non-forest

Circus buffoni	Long-winged Harrier	Non-forest
Circus cinereus	Cinereous Harrier	Non-forest
Colaptes campestris	Campo Flicker	Non-forest
Colaptes melanochloros	Green-barred Woodpecker	Non-forest
Columba livia	Rock Dove	Non-forest
Columbina picui	Picui Dove	Non-forest
Columbina talpacoti	Ruddy Ground-dove	Non-forest
Coragyps atratus	American Black Vulture	Non-forest
Coryphistera alaudina	Lark-like Brushrunner	Non-forest
Coryphospingus cucullatus	Red-crested Finch	Non-forest
Coscoroba coscoroba	Coscoroba Swan	Non-forest
Cranioleuca pyrrhophia	Stripe-crowned Spinetail	Forest
Crotophaga ani	Smooth-billed Ani	Non-forest
Crotophaga major	Greater Ani	Non-forest
Crypturellus tataupa	Tataupa Tinamou	Forest
Crypturellus undulatus	Undulated Tinamou	Forest
Cyanocompsa brissonii	Ultramarine grosbeak	Non-forest
Cyanocorax chrysops	Plush-crested Jay	Forest
Cyclarhis gujanensis	Rufous-browed Peppershrike	Forest
Cypseloides rothschildi	Rothschild's Swift	Non-forest
Drymornis bridgesii	Scimitar-billed Woodcreeper	Non-forest
Dryocopus schulzi	Black-bodied woodpecker	Forest
Egretta thula	Snowy Egret	Non-forest
Elaenia spectabilis	Large Elaenia	Non-forest
Elanus leucurus	White-tailed Kite	Non-forest
Embernagra platensis	Great Pampa-finch	Non-forest
Eudromia formosa	Quebracho Crested Tinamou	Forest
Euphonia chlorotica	Purple-throated Euphonia	Forest
Euphonia cyanocephala	Golden-rumped Euphonia	Forest
Euscarthmus meloryphus	Tawny-crowned Pygmy-tyrant	Non-forest
Falco femoralis	Aplomado Falcon	Non-forest
Falco peregrinus	Peregrine Falcon	Non-forest
Falco rufigularis	Bat Falcon	Forest
Falco sparverius	American Kestrel	Non-forest
Fluvicola pica	Pied Water-tyrant	Non-forest
Furnarius cristatus	Crested Hornero	Forest
Furnarius rufus	Rufous Hornero	Non-forest
Geranoaetus albicaudatus	White-tailed Hawk	Non-forest
Geranoaetus melanoleucus	Black-chested Buzzard-eagle	Non-forest
Geranoaetus polyosoma	Variable Hawk	Non-forest
Geranospiza caerulescens	Crane Hawk	Forest
Glaucidium brasilianum	Ferruginous Pygmy-owl	Forest
Guira guira	Guira Cuckoo	Non-forest
Heliomaster furcifer	Blue-tufted Starthroat	Forest
Hemitriccus margaritaceiventer	Pearly-vented Tody-tyrant	Forest
Herpetotheres cachinnans	Laughing Falcon	Non-forest
Himantopus mexicanus	Black-necked stilt	Non-forest

Hydropsalis torquata	Scissor-tailed Nightjar	Forest
Hylocharis chrysura	Gilded Hummingbird	Non-forest
Icterus icterus	Venezuelan Troupial	Forest
Icterus pyrrhopterus	Variable Oriole	Non-forest
Inezia inornata	Plain Tyrannulet	Forest
Jacana jacana	Wattled Jacana	Non-forest
Knipolegus striaticeps	Cinereous Black-tyrant	Forest
Lepidocolaptes angustirostris	Narrow-billed Woodcreeper	Forest
Leptasthenura platensis	Tufted Tit-spinetail	Forest
Leptotila verreauxi	White-tipped Dove	Forest
Lophonetta specularioides	Crested Duck	Non-forest
Lophospingus pusillus	Black-crested Finch	Non-forest
Machetornis rixosa	Cattle Tyrant	Non-forest
Melanerpes cactorum	White-fronted Woodpecker	Non-forest
Melanerpes candidus	White Woodpecker	Non-forest
Melanopareia maximiliani	Olive-crowned Crescentchest	Non-forest
Milvago chimachima	Yellow-headed Caracara	Non-forest
Milvago chimango	Chimango caracara	Non-forest
Mimus saturninus	Chalk-browed Mockingbird	Non-forest
Molothrus bonariensis	Shiny Cowbird	Non-forest
Molothrus rufoaxillaris	Screaming Cowbird	Non-forest
Mycteria americana	Wood Stork	Non-forest
Myiarchus tyrannulus	Brown-crested Flycatcher	Forest
Myiophobus fasciatus	Bran-colored Flycatcher	Forest
Myiopsitta monachus	Monk Parakeet	Non-forest
Myrmorchilus strigilatus	Stripe-backed Antbird	Forest
Nothoprocta cinerascens	Brushland Tinamou	Non-forest
Nothura maculosa	Spotted Nothura	Non-forest
Nystalus maculatus	Spot-backed Puffbird	Forest
Ortalis canicollis	Chaco Chachalaca	Forest
Pachyramphus viridis	Green-backed Becard	Forest
Parabuteo unicinctus	Harris's Hawk	Forest
Paroaria capitata	Yellow-billed Cardinal	Non-forest
Paroaria coronata	Red-crested Cardinal	Non-forest
Passer domesticus	House Sparrow	Non-forest
Patagioenas cayennensis	Pale-vented Pigeon	Non-forest
Patagioenas maculosa	Spot-winged Pigeon	Non-forest
Patagioenas picazuro	Picazuro Pigeon	Non-forest
Penelope obscura	Dusky-legged Guan	Forest
Phacellodomus ruber	Greater Thornbird	Non-forest
Phacellodomus rufifrons	Rufous-fronted Thornbird	Forest
Phacellodomus sibilatrix	Little Thornbird	Forest
Phacellodomus striaticollis	Freckle-breasted Thornbird	Non-forest
Phaeomyias murina	Mouse-colored Tyrannulet	Forest
Phalacrocorax brasilianus	Neotropical Cormorant	Non-forest
Phyllomyias burmeisteri	Rough-legged Tyrannulet	Forest
Phylloscartes ventralis	Mottle-cheeked Tyrannulet	Forest

Phytotoma rutila	White-tipped Plantcutter	Forest
Piculus chrysochloros	Golden-green Woodpecker	Forest
Picumnus cirratus	White-barred Piculet	Forest
Pipraeidea bonariensis	Blue-and-yellow Tanager	Non-forest
Piranga flava	Red Tanager	Forest
Pitangus sulphuratus	Great Kiskadee	Non-forest
Platalea ajaja	Roseate Spoonbill	Non-forest
Plegadis chihi	White-faced Ibis	Non-forest
Poecilotriccus plumbeiceps	Ochre-faced Tody-flycatcher	Forest
Polioptila dumicola	Masked Gnatcatcher	Non-forest
Poospiza melanoleuca	Black-capped warbling finch	Non-forest
Poospiza torquata	Ringed warbling finch	Non-forest
Psarocolius decumanus	Crested Oropendola	Forest
Pseudocolopterix flaviventris	Warbling doradito	Non-forest
Pseudoseisura lophotes	Brown Cachalote	Forest
Psittacara leucophthalmus	White-eyed Parakeet	Forest
Pyrocephalus rubinus	Common Vermilion Flycatcher	Non-forest
Pyrrhomyias cinnamomeus	Cinnamon Flycatcher	Forest
Ramphastos toco	Toco Toucan	Forest
Rhea americana	Greater Rhea	Non-forest
Rhinocrypta lanceolata	Crested Gallito	Forest
Rhynchospiza strigiceps	Stripe-capped Sparrow	Non-forest
Rhynchotus rufescens	Red-winged Tinamou	Non-forest
Rostrhamus sociabilis	Snail Kite	Non-forest
Rupornis magnirostris	Roadside Hawk	Non-forest
Saltator aurantiirostris	Golden-billed Saltator	Non-forest
Saltator coerulescens	Amazonian Grey Saltator	Non-forest
Saltatricula multicolor	Many-colored Chaco finch	Non-forest
Sarcoramphus papa	King Vulture	Non-forest
Sarkidiornis melanotos	African Comb Duck	Non-forest
Schoeniophylax phryganophilus	Chotoy Spinetail	Non-forest
Serpophaga nigricans	Sooty Tyrannulet	Non-forest
Serpophaga subcristata	White-crested Tyrannulet	Non-forest
Setophaga pitiayumi	Tropical Parula	Forest
Sicalis flaveola	Saffron Finch	Non-forest
Sicalis luteola	Grassland Yellow-finch	Non-forest
Sittasomus griseicapillus	Eastern Olivaceous Woodcreeper	Forest
Spartonoica maluroides	Bay-capped Wren-spinetail	Non-forest
Spinus magellanicus	Hooded Siskin	Non-forest
Spiziapteryx circumcincta	Spot-winged Falconet	Forest
Sporophila collaris	Rusty-collared Seedeater	Non-forest
Sporophila lineola	Lined Seedeater	Non-forest
Sporophila ruficollis	Dark-throated Seedeater	Non-forest
Stigmatura budytoides	Greater Wagtail-tyrant	Non-forest
Sturnella superciliaris	White-browed meadowlark	Non-forest
Sublegatus modestus	Southern Scrub-flycatcher	Forest
Suiriri suiriri	Suiriri Flycatcher	Forest

Synallaxis albescens	Pale-breasted Spinetail	Non-forest
Synallaxis frontalis	Sooty-fronted Spinetail	Forest
Synallaxis spixi	Spix's Spinetail	Non-forest
Syrigma sibilatrix	Whistling Heron	Non-forest
Systellura longirostris	Greater Band-winged Nightjar	Non-forest
Tachycineta leucorrhoa	White-rumped Swallow	Non-forest
Tapera naevia	Striped Cuckoo	Non-forest
Taraba major	Great Antshrike	Non-forest
Tarphonomus certhioides	Chaco Earthcreeper	Forest
Thamnophilus caerulescens	Variable Antshrike	Forest
Thamnophilus doliatus	Barred Antshrike	Forest
Thectocercus acuticaudatus	Blue-crowned parakeet	Non-forest
Theristicus caerulescens	Plumbeous Ibis	Non-forest
Theristicus caudatus	Buff-necked Ibis	Non-forest
Thlypopsis sordida	Orange-headed Tanager	Forest
Thraupis sayaca	Sayaca tanager	Forest
Tigrisoma lineatum	Rufescent Tiger-heron	Non-forest
Troglodytes aedon	House Wren	Non-forest
Trogon curucui	Blue-crowned Trogon	Forest
Turdus amaurochalinus	Creamy-bellied Thrush	Non-forest
Turdus rufiventris	Rufous-bellied Thrush	Forest
Vanellus chilensis	Southern Lapwing	Non-forest
Veniliornis mixtus	Checkered Woodpecker	Forest
Volatinia jacarina	Blue-black Grassquit	Non-forest
Xenopsaris albinucha	White-naped Becard	Non-forest
Xiphocolaptes major	Great Rufous Woodcreeper	Forest
Xolmis irupero	White Monjita	Non-forest
Xolmis rubetra	Rusty-backed Monjita	Non-forest
Zenaida auriculata	Eared Dove	Non-forest
Zonotrichia capensis	Rufous-collared Sparrow	Non-forest

Table SI II-2: List of mammal species recorded in the study area between 2012 and 2015.Mammal species were classified into forest and non-forest species following expert recommendations (Decarre 2015; Gómez-Valencia 2017) and the literature (Canevari & Vaccaro 2007).

Scientific name	**English name**	**Habitat**
Cabassous chacoensis	Chacoan naked-tailed armadillo	Forest
Catagonus wagneri	Chacoan peccary	Forest
Cerdocyon thous	Forest fox	Non-forest
Chaetophractus vellerosus	Small hairy armadillo	Non-forest
Chaetophractus villosus	Larger hairy armadillo	Non-forest
Conepatus chinga	Molina's Hog-Nosed Skunk	Non-forest
Dasypus novemcinctus	Nine-banded armadillo	Non-forest
Didelphis albiventris	White-eared opossum	Non-forest
Eira Barbara	Tayra	Forest
Euphractus sexcinctus	Six-banded armadillo	Non-forest
Galictis cuja	Little grison	Non-forest
Leopardus geoffroyi	Geoffroy's cat	Non-forest
Lepus europaeus	Common hare	Non-forest
Lycalopex gymnocercus	Pampas fox	Non-forest
Mazama gouazoubira	Brown brocket deer	Non-forest
Myrmecophaga tridactyla	Giant anteater	Non-forest
Nasua nasua	South american coati	Forest
Pecari tajacu	Collared peccary	Forest
Priodontes maximus	Giant armadillo	Forest
Puma concolor	Puma	Non-forest
Puma yagouaroundi	Jaguarundi	Non-forest
Sylvilagus brasiliensis	Tapeti	Forest
Tamandua tetradactyla	Collared anteater	Forest
Tapirus terrestris	South american tapir	Forest
Tayassu pecari	White-lipped peccary	Forest
Tolypeutes matacus	Southern three-banded armadillo	Forest

Table SI II-3: Predictor variables and data sources used to explain species richness in the Argentine Dry Chaco for the contemporary period (2009-2013), 2000, and 1985.

Predictors by group	**Name**	**Data Sources**		
		Contemporary	**2000**	**1985**
Landscape structure				
Extent of forest	Forest	Hansen *et al.* (2013) Own calculations	Hansen *et al.* (2013) Own calculations	Baumann *et al.* (2017) Own calculations
Extent of core forest *	Core			
Extent of edge between forested and non-forested patches *	Edge			
Extent of connectivity	Connec			
Aggregation	Aggre			
Human Disturbance				
Distance to big settlements	DistTown	www.indec.gob.ar	www.indec.gob.ar	www.indec.gob.ar
Distance to *puestos*	DistPuesto	Landsat images and Google Earth; Grau, Gasparri and Aide (2008)	Landsat images and Google Earth; Grau, Gasparri and Aide (2008)	Landsat images and Google Earth; Grau, Gasparri and Aide (2008)
Distance to paved roads	DistRoad	www.ign.gob.ar	Atlas de Rutas Firestone	Atlas de la República Argentina, IGM
Density non-paved roads	DensRoad	www.ign.gob.ar	www.ign.gob.ar	www.ign.gob.ar
Climate †				
Long-term temperature	Temp			
Long-term precipitation	Prec	INTA weather stations	INTA weather stations	INTA weather stations
Aridity ‡	Aridity			
Water Availability				
Density rivers ¶	DensRiver	www.ign.gob.ar	www.ign.gob.ar	www.ign.gob.ar
Distance to water bodies	DistWater			

* We used a 300-m edge width to calculate core area and edges, following edge effects literature for birds and mammals (Debinski & Holt 2000; Laurance *et al.* 2002; Ribeiro *et al.* 2009).

† INTA weather stations consist of point data. We interpolated the point data to obtain a continuous maps for our study area using Kriging in ArcGIS.

‡ Aridity index was calculated by dividing precipitation by evapotranspiration.

¶ We did not include this variable in the mammals analyses as the areas where mammals were sampled contained very few rivers.

Table SI II-4: Candidate models explaining bird species richness in the study area for the three periods of time and the variables included (i.e., not correlated) (x) in each model.Full models test for the relative importance of landscape structure variables vs. other factors (human disturbance, climate and water availability). Models excluding landscape structure (noLS) assume that biodiversity is not affected by landscape structure. The forest species (hurdle) models contain two nested models: a pa model (presence-absence data) and a p model (presence-only data). Correlated variables (r >0.6) were excluded from these models.

Model	**Explanatory Variables**												
	Landscape Structure				**Human Disturbance**				**Climate**			**Water availability**	
	Forest	Core	Edge	Connec	DistTown	DistRoad	DensRoad	DisPuesto	Temp	Prec	Aridity	DensRiver	DistWater
All species													
Bird_contemp_full		x	x	x	x	x	x	x		x	x	x	x
Bird_contemp_noLS					x	x	x	x		x	x	x	x
Bird_2000_full		x	x	x	x	x	x	x	x	x	x	x	x
Bird_2000_noLS					x	x	x	x	x	x	x	x	x
Bird_1985_full		x	x		x	x	x	x		x	x	x	x
Bird_1985_noLS					x	x	x	x		x	x	x	x
Forest species													
BirdFor_contemp_full_pa		x	x	x	x	x	x	x		x	x	x	x
BirdFor_contemp_full_p		x	x	x	x	x	x	x		x	x	x	x
BirdFor_contemp_noLS_pa					x	x	x	x		x	x	x	x
BirdFor_contemp_noLS_p					x	x	x	x		x	x	x	x
BirdFor_2000_full_pa		x	x	x	x	x	x	x	x	x	x	x	x
BirdFor_2000_full_p		x	x	x	x	x	x	x	x	x	x	x	x
BirdFor_2000_noLS_pa					x	x	x	x	x	x	x	x	x
BirdFor_2000_noLS_p					x	x	x	x	x	x	x	x	x
BirdFor_1985_full_pa		x	x		x	x	x	x		x	x	x	x
BirdFor_1985_full_p		x	x		x		x	x		x	x	x	x
BirdFor_1985_noLS_pa					x	x	x	x		x	x	x	x
BirdFor_1985_noLS_p					x		x	x		x	x	x	x

Table SI II-5: Candidate models explaining mammal species richness in the study area for the three periods of time and the variables included (i.e., not correlated) (x) in each model. Full models test for the relative importance of landscape structure variables vs. other factors (human disturbance, climate and water availability). Models excluding landscape structure (noLS) assume that biodiversity is not affected by landscape structure. The forest species (hurdle) models contain two nested models: a pa model (presence-absence data) and a p model (presence-only data). Correlated variables (r > 0.6) were excluded from these models.

Model	Explanatory Variables											
		Landscape Structure				Human Disturbance				Climate		Water Availability
	Forest	Core	Edge	Connec	DistTown	DistRoad	DensRoad	DisPuesto	Temp	Prec	Arid	DistWater
All species												
Mam_contemp_full		x	x	x		x	x				x	x
Mam_contemp_noLS						x	x				x	x
Mam_2000_full		x	x			x	x	x		x	x	x
Mam_2000_noLS						x	x	x		x	x	x
Mam_1985_full		x				x					x	x
Mam_1985_noLS						x					x	x
Forest species												
MamFor_contemp_full_pa		x	x	x		x	x				x	x
MamFor_contemp_full_p		x	x				x				x	x
MamFor_contemp_noLS_pa						x	x				x	x
MamFor_contemp_noLS_p							x				x	x
MamFor_2000_full_pa		x	x			x	x	x		x	x	x
MamFor_2000_full_p		x	x			x				x	x	x
MamFor_2000_noLS_pa						x	x	x		x	x	x
MamFor_2000_noLS_p						x				x	x	x
MamFor_1985_full_pa		x				x					x	x
MamFor_1985_full_p		x									x	x
MamFor_1985_noLS_pa						x					x	x
MamFor_1985_noLS_p											x	x

Figure SI II-1: Sample coverage (i.e., the proportion of species present in the sample) for bird species richness as a function of sampling effort Dashed lines indicate the 95% confident intervals. The curve was generated using R package *iNEXT* (Hsieh, Ma & Chao 2016) and it shows how the sample coverage does not increase substantially when increasing the sampling effort (i.e., the number of point counts).

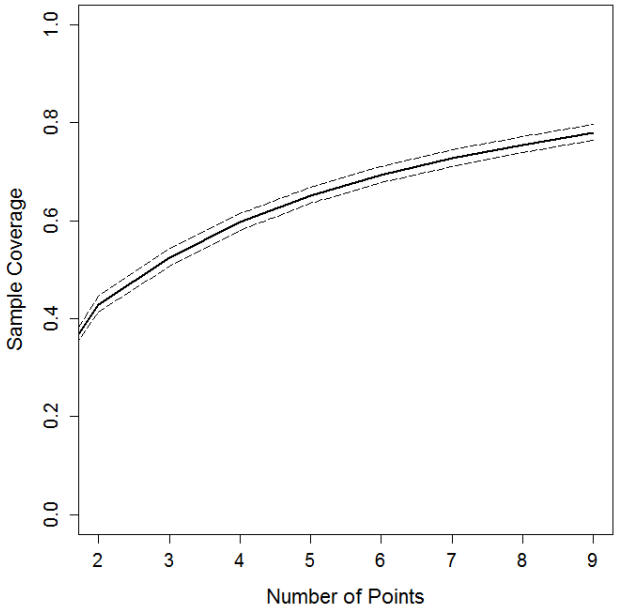


Figure SI II-2: Relation between rarefied and original richness for (a) bird, (b) bird forest, (c) mammal and (d) mammal forest species. Points on the line present the same value for the original than for the rarefied richness.

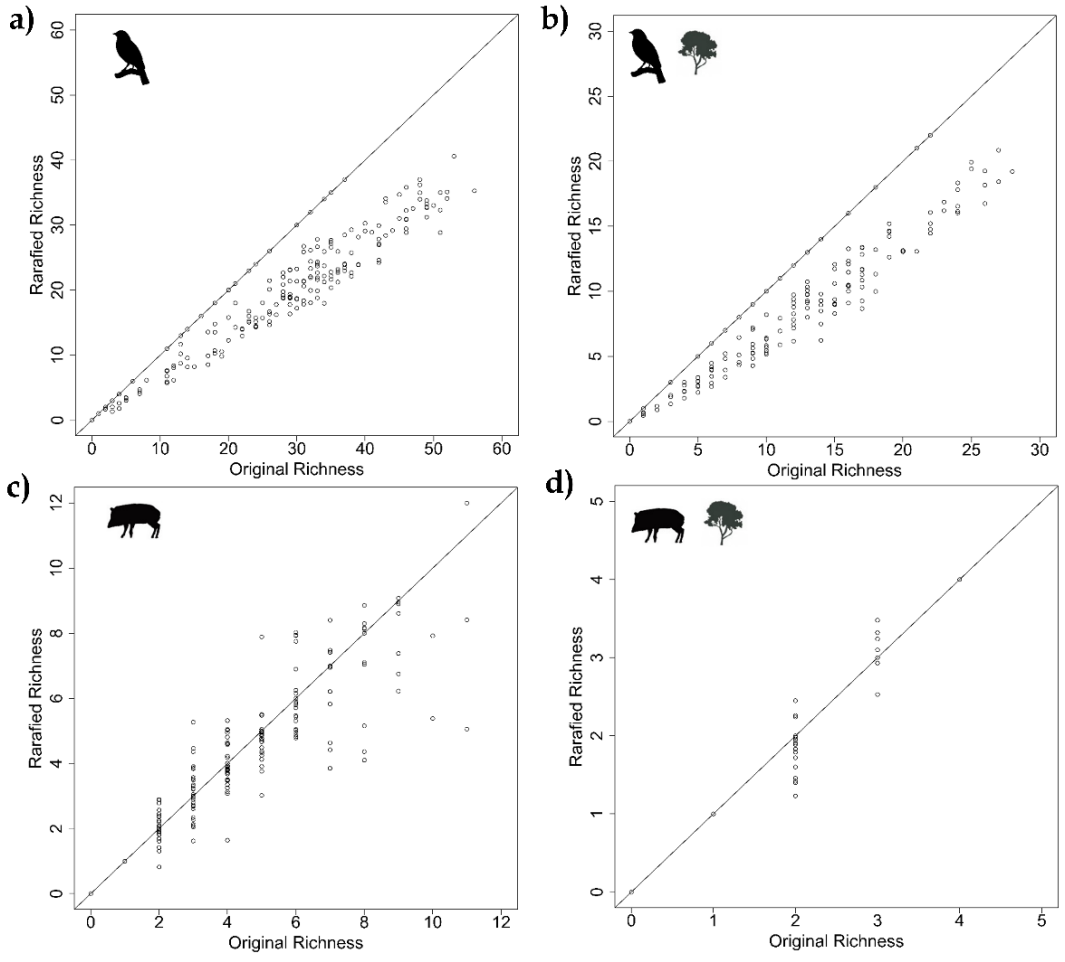


Figure SI II-3: Share of the study region categorized as having high (future decrease >20% compared to contemporary richness) and low extinction debt (future decrease 20%-5%)

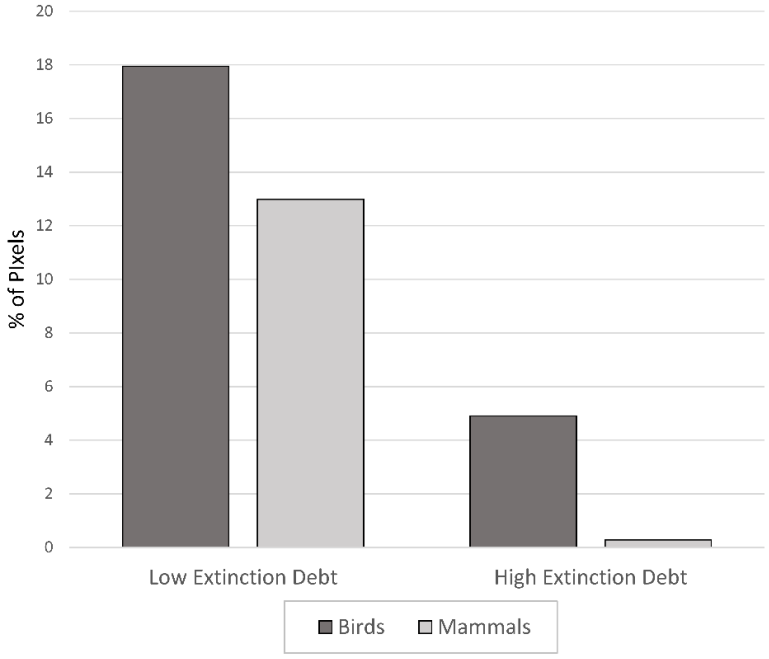


Figure SI II-4: Estimated extinction debt for birds when rarefying species richness to a) 4 point counts, b) 6 point counts and c) 9 point counts. The three maps show the same spatial patterns (i.e., extinction debt is likely to occur in the same areas), however the predicted number of species to go extinct is higher when rarefying to 9 and 6 points, as opposed to 4 points.

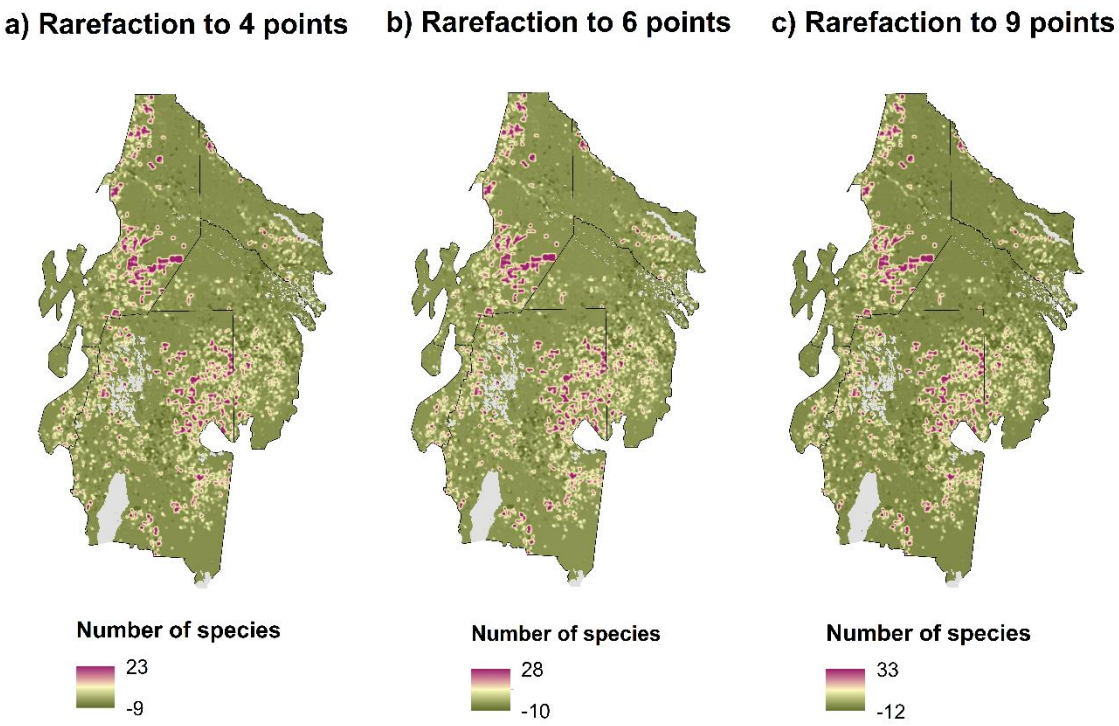


Figure SI II-5: Predicted number of bird species at the contemporary time under an extinction debt scenario (a), and without an extinction debt scenario (b). Predicting the number of species without considering future local extinctions as a consequence of past land-use changes (i.e., map without an extinction debt scenario) overestimates the number of species compared to the predicted number of species under an extinction debt scenario.

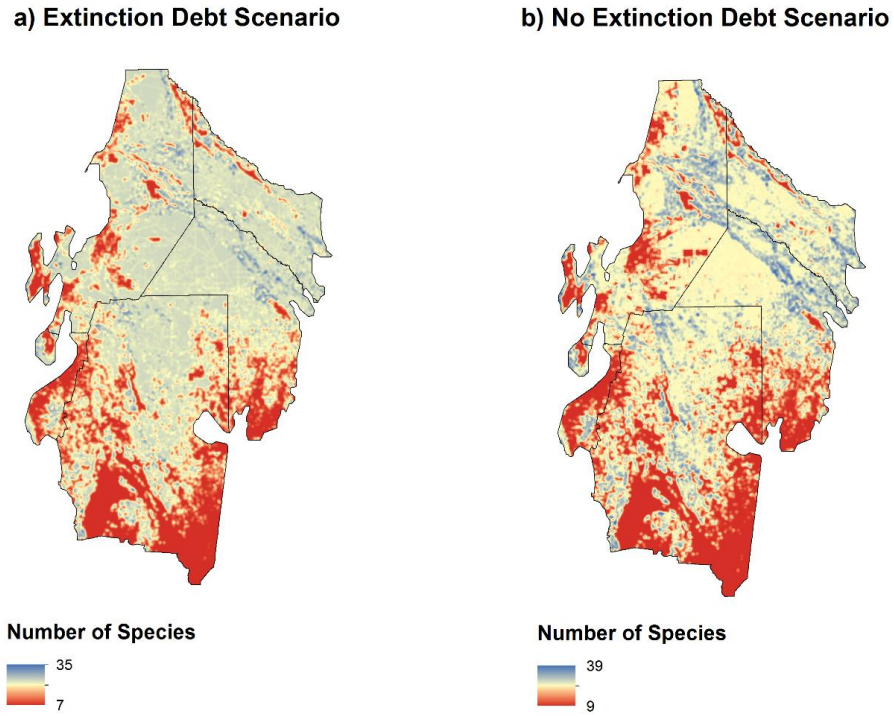
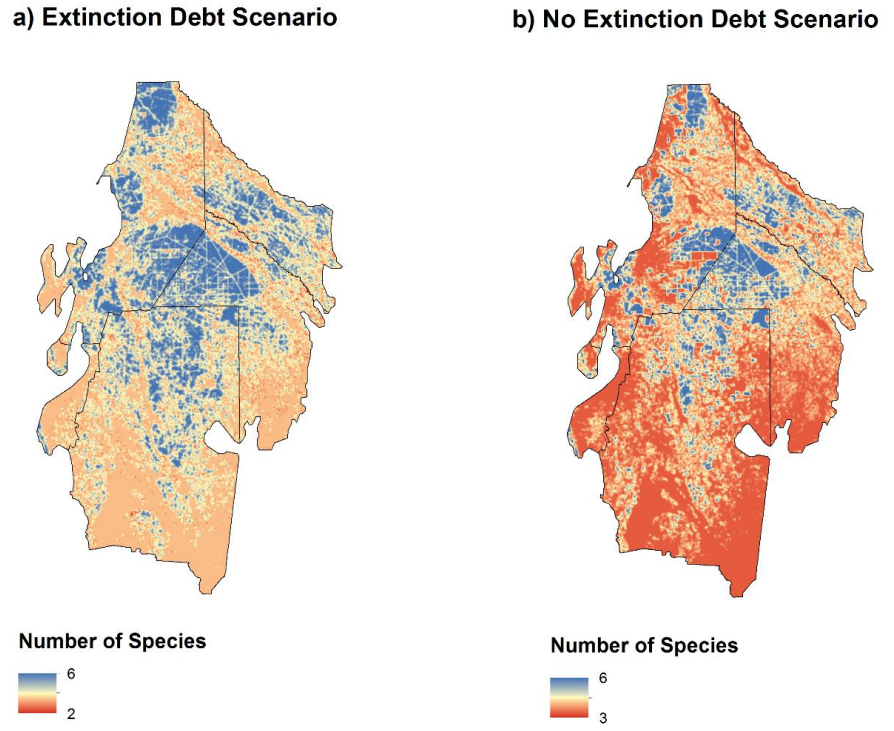


Figure SI II-6: Predicted number of mammal species at the contemporary time under an extinction debt scenario (a), and without an extinction debt scenario (b).Predicting the number of species without considering future local extinctions as a consequence of past land-use changes (i.e., map without an extinction debt scenario) overestimates the number of species compared to the predicted number of species under an extinction debt scenario.



Chapter III:

How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change?

(in review)

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Abstract

Land-use change is a root cause of the extinction crisis, but links between habitat change and biodiversity loss are not fully understood. While there is evidence that habitat loss is an important extinction driver, the relevance of habitat fragmentation remains debated. Moreover, while time-delays of biodiversity responses to habitat transformation are well-documented, time-delayed effects have been ignored in the habitat loss vs. fragmentation debate. Here, using a hierarchical Bayesian multi-species occupancy framework, we systematically tested for time-delayed responses of bird and mammal communities to habitat loss and to habitat fragmentation. We focused on the Argentine Chaco, where deforestation has been widespread recently. We used an extensive field dataset on birds and mammals, along with a time series of annual woodland maps from 1985-2016 covering recent and historical habitat transformations. Contemporary habitat amount explained bird and mammal occupancy better than past habitat amount. However, occupancy was affected more by past rather than recent fragmentation, indicating a time-delayed response to fragmentation. Considering past landscape patterns is therefore crucial for understanding current biodiversity patterns. Not accounting for land-use history ignores the possibility of extinction debt and can thus obscure impacts of fragmentation, potentially explaining contrasting findings of habitat loss vs. fragmentation studies.

1 Introduction

Land-use change is a main driver of biodiversity loss, primarily via loss and fragmentation of habitat (Tilman *et al.* 2017). Where habitat is lost, species' populations decline and might eventually go extinct; a phenomenon widely observed (Brooks *et al.* 2002; Fahrig 2013) and with strong theoretical underpinnings in population ecology (Wiegand, Revilla & Moloney 2005). Additionally, as habitat is lost, landscapes become more fragmented, containing higher numbers of typically smaller and more isolated patches (Fahrig 2003). Metapopulation theory (Hanski 1998) and island biogeography theory (MacArthur & Wilson 1967) suggest that fragmentation negatively impacts species' populations and overall species richness. Finally, fragmented landscapes contain more edge habitat (Broadbent *et al.* 2008), which exerts pressure on many species, for instance by degrading habitat quality, altering biophysical conditions, changing species interactions, or increasing human-wildlife conflicts (Laurance *et al.* 2002; Fahrig 2003; Pfeifer *et al.* 2017).

Yet, edge habitats also increase landscape heterogeneity, and therefore, species richness may increase near edges (Fahrig 2017). Recent reviews indicate that the effect of habitat fragmentation on biodiversity, independent of habitat amount, is weak and could even be positive sometimes (Fahrig 2013; Fahrig 2017; Watling *et al.* 2020). This suggests that species primarily respond to the extent of habitat in the landscape (i.e., the habitat amount hypothesis (Fahrig 2013)), and not to fragmentation (i.e., habitat patch configuration). The resulting debate about the relative importance of habitat fragmentation, and whether the effects of fragmentation on biodiversity are negative or positive, has been heated (Fahrig 2013; Melo *et al.* 2017; Fletcher Jr *et al.* 2018; Fahrig *et al.* 2019). This debate has potentially major consequences for conservation (Miller-Rushing *et al.* 2019). If fragmentation affects biodiversity negatively, protecting large habitat patches, and corridors between them, should be prioritized (Worboys, Francis & Lockwood 2010). To the contrary, if habitat amount is the main determinant of biodiversity, several small habitat patches will have the same conservation value as an equally large, single patch (Fahrig 2017; Fahrig 2020; Watling *et al.* 2020), and greater emphasis should be put on protecting the largest amount of habitat, regardless of connectivity and patch size.

Available evidence on the relative effects of habitat amount vs. fragmentation on biodiversity, however, remains inconclusive (Miller-Rushing *et al.* 2019), especially at broader spatial scales (Fahrig *et al.* 2019). Several factors contribute to this. First, fragmentation effects may differ at the patch scale vs. landscape scale, because some processes acting at landscape scales cannot be captured when studying individual patches

(e.g., interactions with wide-ranging species, habitat diversity across patches). Second, different effects can be found when focusing on habitat specialists (e.g., forest-dependent species) vs. generalists or the entire community (Pfeifer *et al.* 2017). Third, fragmentation effects consist of edge effects and isolation effects, and focusing on only one aspect may not capture the full impact of fragmentation (Ewers & Didham 2006; Haddad *et al.* 2015). Finally, the time period over which habitat fragmentation is studied may greatly impact conclusions (Haddad *et al.* 2015; Miller-Rushing *et al.* 2019), yet most studies are based on contemporary landscape data.

This focus only on contemporary landscapes is particularly worrisome given increasing evidence for time-delayed responses of biodiversity to habitat transformation (Kuussaari *et al.* 2009; Krauss *et al.* 2010; Semper-Pascual *et al.* 2018; Lira, de Souza Leite & Metzger 2019). Species do not always react to habitat transformation immediately, and may persist for decades in transformed landscapes (Kuussaari *et al.* 2009). Such time-delayed responses can create extinction debt, i.e., number or proportion of extant species predicted to go extinct due to past landscape transformation (Tilman *et al.* 1994). The probability of communities showing time-delayed responses depends on species' life-history traits, as well as other factors related to landscape transformation (e.g., magnitude of landscape change or time since transformation (Kuussaari *et al.* 2009; Figueiredo *et al.* 2019)). Understanding time-delayed responses and extinction debt is critical to delineating a window of time for conservation to avert such extinctions (Kuussaari *et al.* 2009). Surprisingly though, most fragmentation studies have ignored time-delayed effects (Ewers & Didham 2006; Fletcher Jr *et al.* 2018).

A typical limitation of studies that have investigated time-delayed effects of habitat loss and fragmentation on biodiversity, is that they assessed land-use change on only one or a few snapshots in time, typically with long periods between them (Metzger *et al.* 2009; Krauss *et al.* 2010; Uezu & Metzger 2016). However, land-use change often occurs gradually, meaning that estimated time-delayed responses might remain undetected or appear to be overly long when considering few snapshots. Previous studies also typically assumed that time-delayed response is the same for habitat loss and habitat fragmentation. This is potentially problematic because the effects of past habitat loss may be more immediate than those of fragmentation. In fact, long-term fragmentation experiments found effects of fragmentation to magnify over time (Haddad *et al.* 2015; Crooks *et al.* 2017). To our knowledge, no study has investigated whether time-delayed responses of biodiversity to habitat loss and habitat fragmentation differ.

Advances in satellite data availability and processing now allow for reconstructing landscape change at high spatial and temporal resolutions (Oeser *et al.* 2019). Here, using the Landsat archive since 1985, we systematically test for time-delayed effects of habitat loss and habitat fragmentation on birds and mammals in the Argentine Dry Chaco over a period of 31 years. The Chaco provides an interesting case study due to its dynamic land-use history and recent high deforestation rates (Baumann *et al.* 2017). We assessed two research questions:

1. Are contemporary or past landscape patterns more important in determining contemporary bird and mammal communities?
2. Are time-delayed responses more prominent for habitat loss or habitat fragmentation?

We predicted that contemporary bird and mammal communities would be affected by past landscape patterns, because extinction debts are likely to not yet be paid in landscapes where habitat transformation has occurred recently, such as the Chaco. We also predicted that time-delayed responses would be more prominent for habitat fragmentation as the effects of habitat fragmentation can take a long time to manifest on the landscape.

2 Methods

2.1 Study area

The Gran Chaco is the largest subtropical/tropical dry forest in South America, covering parts of Argentina, Paraguay, Bolivia and Brazil. The region is rich in biodiversity, harboring over 500 birds, 150 mammals, 120 reptiles and 100 amphibians (TNC *et al.* 2005). We focused on the Argentine Dry Chaco (~21 million ha, Figure III-1), an area with a highly seasonal climate (precipitation: from 450 to 900mm; temperature: -7°C to +42°C) (Minetti *et al.* 1999). Natural vegetation is dominated by woodlands with a few interspersed natural grasslands (Baumann *et al.* 2018). Much of the regions' natural vegetation has been converted to agriculture, especially after 2000, mainly for cattle ranching and soybean cultivation (Fehlenberg *et al.* 2017). This has resulted in widespread woodland loss and fragmentation (Piquer-Rodríguez *et al.* 2015; Baumann *et al.* 2018), which in turn has been a main cause of defaunation (Periago, Chillo & Ojeda 2015; Semper-Pascual *et al.* 2018).

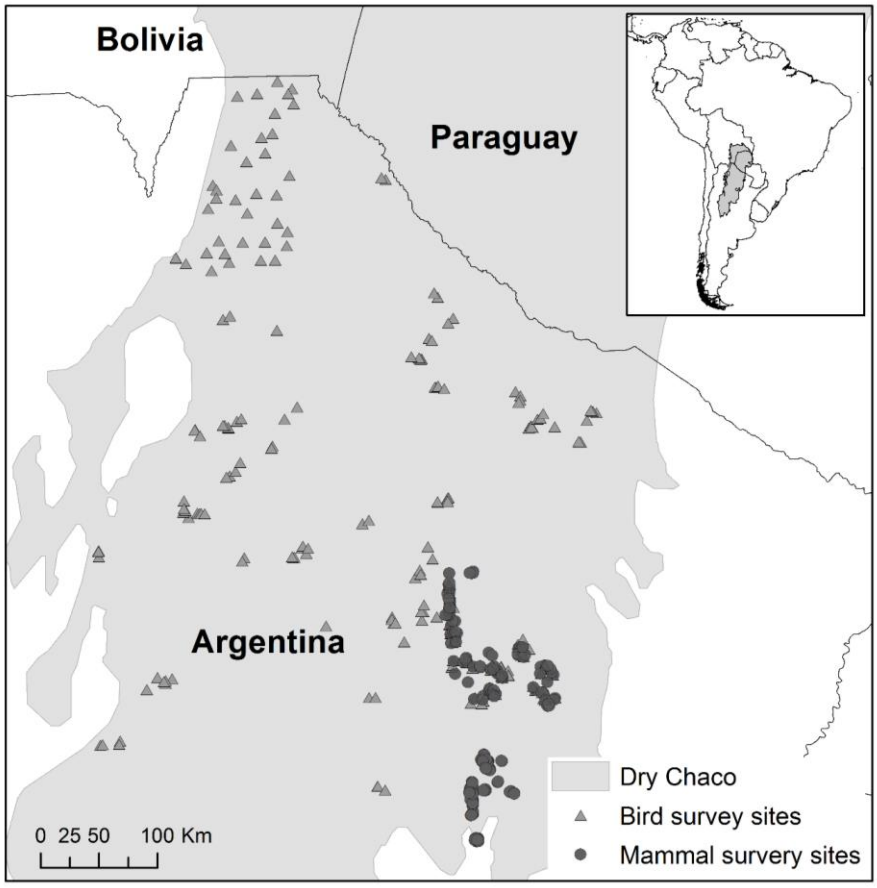


Figure III-1: Survey sites for birds and mammals in the northern Argentine Dry Chaco.

2.2 Biodiversity data

We surveyed birds and mammals at 431 sites (Figure III-1) selected to represent gradients of land use and woodland cover. We recorded birds at 233 sites during three field surveys between 2009 and 2014 (Mastrangelo & Gavin 2012; Macchi *et al.* 2013; Decarre 2015), with a mean distance of 4.7-km between sites (standard deviation: SD=6.5-km). We conducted point counts at each site (two to nine point counts per site; Text SI III-1). Here, we only considered species that use woodland as their main habitat, as this is the dominant natural vegetation in the area and we wanted to test for time-delayed responses to woodland loss and fragmentation. We discarded migrant species to avoid seasonal effects and species associated with the Andean Cloud forest (i.e., Yungas) that were only recorded in the Chaco-Yungas ecotone.

We surveyed mammals during two field surveys between 2013 and 2016, using a total of 198 camera-trap stations (Decarre 2015; Gómez-Valencia 2017). The mean distance between adjacent sites was 1.44-km (SD=1.74). We set cameras off trail where possible, to reduce detection bias associated with targeted sampling (Kolowski & Forrester 2017). Cameras

were active between 14 and 84 trapping days (mean=39.8 days), with a total sampling effort of 7,883 trapping days (Text SI III-2). We only considered woodland-dependent mammal species.

We did not assess spatial autocorrelation among sampling sites, as common tests (e.g., spatial correlograms of model residuals) are difficult to apply in an occupancy framework (MacKenzie *et al.* 2006; Burton *et al.* 2012). However, spatial autocorrelation is not a problem, as the independence assumption of occupancy models relates to the observation process, not to the occupancy process, and it can be accounted for with an appropriate sampling design (e.g., random sampling, as in our case) (MacKenzie *et al.* 2017). Additionally, overlapping landscapes have been shown to not violate the independence assumption (Zuckerberg *et al.* 2020).

2.3 Landscape predictors

We calculated landscape-scale metrics of habitat amount and fragmentation, meaning that they described the spatial characteristics of entire landscapes, not individual patches (Fahrig 2017). We extracted predictors for circular landscapes centered around each sampling site. Based on sensitivity analyses (Text SI III-3), we used a 4-km radius for birds, and a 2-km radius for mammals. For each of the circular landscapes, we mapped woodland cover for each year between 1985 and 2016 based on Landsat composite metrics derived at a spatial resolution of 30-m in Google Earth Engine (Gorelick *et al.* 2017). We used an extensive database of training samples (Baumann *et al.* 2017) and hand-digitized deforestation polygons between 2014 and 2016 from GUYRA Paraguay (http://guyra.org.py/informedeforestacion). We used these training data to parameterize a time-calibrated random forest classifier, and classified 31 annual woodland loss maps between 1985 and 2016 (Griffiths, Jakimow & Hostert 2018). Each map used satellite data from that year and the previous year, to ensure consistency between years. We validated these maps following best-practice procedures (Olofsson *et al.* 2014) (average overall accuracy = 90%; standard error = 0.6%, Text SI III-4 and Figure SI III-1).

We calculated one landscape predictor representing habitat amount: *percentage of woodland*. To characterize fragmentation, we calculated three predictors: *percentage of edge*, *patch density* and *cohesion index*. A detailed description of these landscape metrics is provided in Figure III-2 and Text SI III-5. We calculated all metrics for each landscape and for every year between 1985 (first woodland map) and 2016 (last year of biodiversity sampling). To define the contemporary time period, we related each site to the landscape predictors of the

year when biodiversity was sampled (e.g., sites sampled in 2015 were related to the predictors from 2015). We then derived a time series of past landscape predictors 24 years back in time (i.e., landscape patterns from 1 year prior to sampling, 2 years prior to sampling, etc.). We used a maximum time period of 24 years because this is the time span between the oldest Landsat-based woodland map (1985) and the oldest biodiversity sampling (2009) in our dataset.

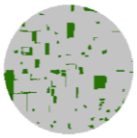
Landscape metric	Definition	Low	Medium	High
HABITAT LOSS				
Percentage of woodland	Measures the amount of habitat in the landscape			
HABITAT FRAGMENTATION				
Percentage of edge	Measures the proportion of edge habitat in the landscape			
Patch density	Measures the number of patches in the landsacpe			
Cohesion index	Measures the structural connectedness of patches in the landscape			

Figure III-2: Landscape metrics used to measure habitat amount and habitat fragmentation in our landscapes (4-km buffers for birds, 2-km buffers for mammals; green = woodland; grey = matrix). Further description on metrics calculation is provided in Text SI III-5.

2.4 Modelling framework

We used hierarchical Bayesian multi-species occupancy models (Dorazio & Royle 2005; Burton *et al.* 2012) to assess the influence of our landscape predictors on bird and mammal communities. Occupancy models estimate detection probability, providing a key advantage when working with elusive species. Estimating detection probability requires sites to be visited on multiple occasions within a period closed to changes in occupancy (MacKenzie *et al.* 2017). For mammals, we defined a sampling occasion as seven consecutive camera-days (Semper-Pascual *et al.* 2019; Semper-Pascual *et al.* 2020). We discarded sites surveyed <14 camera-days to have a minimum of two occasions per site, and assumed communities to be closed (no site-level species extinction or colonization) for a maximum of 12 sampling

occasions (84 days). This resulted in an average of 5.69 occasions (SD=3.07). For birds, we used spatial occasions instead of temporal occasions by treating each point count as one sampling occasion (MacKenzie *et al.* 2017). This resulted in an average of 7.21 occasions (SD=2.26).

Multi-species occupancy models are an extension of single-species occupancy models (MacKenzie *et al.* 2002), in which community occupancy is estimated from the occupancy of all individual species, and where species-specific parameters are drawn from a common, community-level distribution. We used data augmentation to account for species that could theoretically be present but were unobserved (Dorazio & Royle 2005). Based on the literature (Short 1975; Canevari & Vaccaro 2007; Del Hoyo *et al.* 2014), and species observed during other field surveys, we added eight bird and two mammal species (Table SI III-1and Table SI III-2).

Our hierarchical community model therefore had three levels: 1) a level related to the augmented community, in which the occurrence of observed or unobserved species k (w_k) is represented by a Bernoulli process ($w_k \sim$ Bernoulli [Ω], where Ω indicates the probability of a species belonging to the sampled community); 2) an ecological process in which the true occurrence of species k at site i (z_{ik}) is a latent state variable represented by a Bernoulli process ($z_{ik} \sim$ Bernoulli [$w_k * \Psi_{ik}$], Ψ_{ik} represents the occupancy probability); 3) an observation process, in which the detection of species k for occasion j at site i is represented by a Bernoulli process ($y_{ijk} \sim$ Bernoulli [$z_{ik} * p_{ijk}$], p_{ijk} represents the detection probability and is conditional on the site being occupied, i.e., $z_{ik} = 1$).

Occupancy and detection probabilities therefore varied by species and were additionally influenced by site characteristics. We first fitted the detection model by including only predictors that may affect detection, using a null occupancy model with no parameters. For birds, we used *observer* and *openness*, and for mammals, we included *camera-trap*, *sampling effort*, *temperature* and *precipitation* as predictors influencing detection (Table III-1). After excluding correlated predictors (Table III-1), we compared all possible detection models using the Watanabe-Akaike information criterion (WAIC) (Watanabe 2010). Next, we fitted the occupancy model by adding landscape predictors while keeping the best-fitting detection model constant. We used uninformative priors and ran 10 parallel chains of 100,000 Markov Chain Monte Carlo (MCMC) iterations, discarding the first 50,000 iterations as the burn-in process and thinning by 10. We assessed model convergence using visual inspection (trace and density plots of MCMC chains) and the Gelman-Rubin

statistic, where values <1.1 indicated convergence (Gelman *et al.* 2013). Model codes are provided in Text SI III-6 and Text SI III-7.

Table III-1: Predictors used for modelling the detection probability of birds and mammals in the Argentine Chaco.

Predictor	Description	Hypothesis
Birds		
Survey	Observer identity	Experience and knowledge of the observers may influence detection probabilities
Openness	Presence or absence of trees at the sampling site	Presence of trees may decrease detection probability
Mammals		
Camera-trap	Camera-trap survey	Different camera-trap brands and deployments may lead to different detection probabilities
Sampling effort	Number of days that the camera-traps were active	Detection probability increases with increasing survey effort
Temperature*	Mean temperature of the month when the cameras were active	Mammals may be less active when it is too cold or too hot, thus decreasing detection probability
Temperature (quadratic form)*	Mean temperature of the month when the camera-trap was active	Mammals may be less active during extreme temperatures (i.e., too hot and cold), thus decreasing detection probability
Precipitation*	Mean precipitation of the month when the camera-trap was active and the month before	Mammals may move more during the dry season looking for water, thus increasing detection probability

Predictors marked with a * were correlated (r>0.60). We retained *precipitation*, as it had the lowest WAIC in a univariate model.

2.5 Exploring time-delayed responses to habitat loss and fragmentation

To test whether bird and mammal communities showed time-delayed responses to habitat loss and habitat fragmentation, we analyzed the relationships between contemporary community occupancy probability (i.e., mean occupancy across all species) and (1) contemporary landscape predictors (i.e., year of biodiversity sampling) and (2) past landscape predictors (i.e., 1-24 years prior to sampling). We investigated each landscape predictor individually in terms of its influence on community occupancy separately for birds and mammals. We built 25 univariate models for each landscape predictor and taxon: one model including the landscape predictor of the year when biodiversity was sampled (contemporary model) and 24 models using past landscape predictors. As a result, we fitted 200 models; 100 models (25 years x 4 landscape predictors) per taxon (Table SI III-3 and Table SI III-4). To assess which model out of the 25 models for each landscape predictor performed best, we compared them by calculating WAIC for each model. We additionally fitted a smooth line to the WAIC values by using the locally estimated scatterplot smoothing method, to visualize the trend in model performance across years. We inferred a time-delayed response to habitat loss or habitat fragmentation when any of the past models fitted better than the contemporary model (Kuussaari *et al.* 2009; Krauss *et al.* 2010; Semper-Pascual *et*

al. 2018) (Figure III-3). Finally, we assessed the effects of habitat amount and habitat fragmentation on birds and mammals by examining the beta coefficients of our univariate models.

We additionally built three bivariate models which included *percentage of woodland* and a fragmentation metric (*percentage of edge* or *patch density* or *cohesion index*). This allowed us to estimate the effect of habitat amount, while accounting for the effect of habitat fragmentation and vice versa. We built the bivariate models using a) contemporary landscape predictors (i.e., year of biodiversity sampling), and b) predictors of the best-fitting models (i.e., predictors of the univariate models with the lowest WAIC).

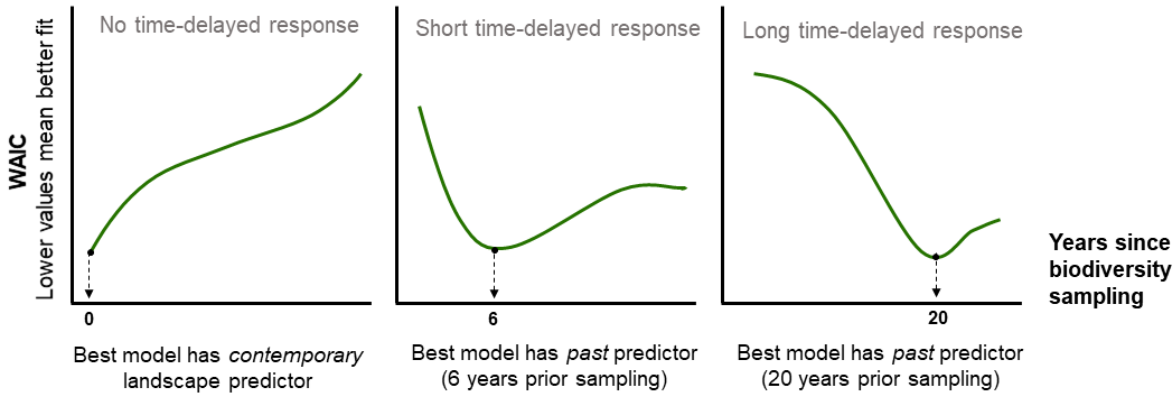


Figure III-3: Approach for assessing time-delayed responses to habitat loss and habitat fragmentation. We concluded that a time-delayed response to habitat loss or to habitat fragmentation was present when any of the models including past landscape predictors (i.e., 1-24 years prior to biodiversity sampling) fitted better (i.e., lower WAIC) than the contemporary model (i.e., predictors from the year of biodiversity sampling).

3 Results

We detected a total of 29 woodland-dependent bird species and 18 woodland-dependent mammal species (Table SI III-1 and Table SI III-2). The best-fitting detection model for the bird dataset included *survey* and *openness* (Table SI III-5). The probability of detecting a bird species, given its occurrence at a site, varied among the three surveys, and increased when trees were present at the sampling site (β = 2.21; 95% Bayesian credible intervals (CRI) = 1.93, 2.52). For mammals, the best-fitting detection model contained *camera-trap* and *precipitation* (Table SI III-5), indicating that detection probability varied depending on camera-trap brand and set-up at the sampling site, and increased with increasing precipitation (β = 0.11; 95% CRI = -0.03, 0.29).

For habitat amount, we found that community-level occupancy probabilities for bird and mammal communities were more strongly influenced by contemporary habitat amount than

by past habitat amount (Figure III-4). The model including contemporary *percentage of woodland* (i.e., year of biodiversity sampling) had the lowest WAIC for birds (Table SI III-3). For mammals, the model with the lowest WAIC included *percentage of woodland* from 1 year prior to sampling, followed by the model including contemporary *percentage of woodland* (Table SI III-4). *Percentage of woodland* was positively related to bird and mammal occupancy (Figure III-5).

Regarding the temporal effect of habitat fragmentation, past fragmentation predictors explained bird and mammal occupancy better than did contemporary fragmentation predictors in most cases. For birds and *percentage of edge*, models including variables from 12 and 13 years prior to sampling were the best models (i.e., lowest WAIC; Figure III-4 and Table SI III-3). For *patch density*, the model including the landscape metric from 4 years prior to sampling had the lowest WAIC values (Figure III-4 and Table SI III-3). For *cohesion index*, the bird occupancy models based on past landscapes (from 4 to 24 years prior to sampling) were consistently better than the models including contemporary landscapes, with the model including cohesion index from 23 years prior to sampling having the lowest WAIC value (Figure III-4 and Table SI III-3). For mammals, models based on *percentage of edge* for past landscapes had a lower WAIC than the model including contemporary *percentage of edge*, with the model with *percentage of edge* from 6 years prior to sampling having the lowest WAIC (Figure III-4 and Table SI III-4). Past *patch density* (specifically from 6 years prior to sampling) also explained contemporary mammal occupancy better than contemporary patch density (Figure III-4 and Table SI III-4). Finally, contemporary *cohesion index* was a better predictor of mammal occupancy than any *cohesion index* for past landscape configurations (Figure III-4 and Table SI III-4).

The effect of habitat fragmentation on occupancy varied depending on the taxa and landscape metric. The effect of *percentage of edge* on bird occupancy changed from negative to positive when adding *percentage of woodland* to the model, i.e., in the bivariate model (Figure III-5). For mammals however, the effect of edge was always negative (both in the univariate and bivariate model), indicating that occupancy decreased with increasing edge habitat (Figure III-5). For both birds and mammals, the effect of *patch density* also changed from negative in the univariate model (i.e., occupancy was lower in patchier landscapes) to positive in the bivariate model (i.e., occupancy was higher in patchier landscapes) (Figure III-5). Finally, *cohesion index* always (i.e., univariate and bivariate model) had a positive effect on occupancy, indicating that the probability of occupancy increased in more connected landscapes (Figure III-5).

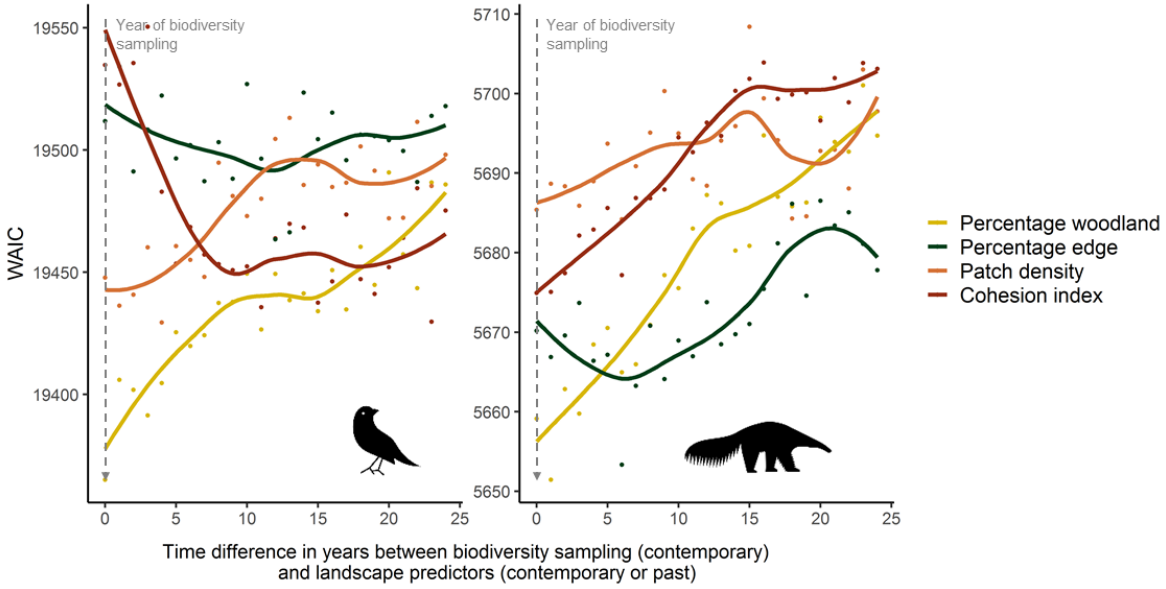


Figure III-4: Model performance of the annual multi-species occupancy models for birds (left) and mammals (right). Model performance is measured using the Watanabe-Akaike information Criterion (WAIC), and thus, lower values indicate higher performance. Each graph shows the performance of models using contemporary biodiversity data, and contemporary (year 0) or past (year 1-24) landscape variables. A smooth line fitted to the WAIC values visualizes the trend in model performance for models with landscapes variables from landscapes increasingly longer ago.

4 Discussion

Habitat loss is a main driver of biodiversity loss, but the importance of habitat fragmentation remains debated (Miller-Rushing *et al.* 2019). Available evidence regarding fragmentation effects remains inconclusive despite considerable research efforts (Fahrig 2013; Haddad *et al.* 2017; Fletcher Jr *et al.* 2018). Yet understanding the impact of fragmentation is critically important, given that land-use change has fragmented most ecosystems around the globe (Haddad *et al.* 2015; Crooks *et al.* 2017). Time-delayed effects of fragmentation are a possible explanation for contrasting results of fragmentation studies, but remain overlooked in the habitat loss vs. fragmentation debate (Fletcher Jr *et al.* 2018; Miller-Rushing *et al.* 2019).

We provide, to the best of our knowledge, the first systematic assessment of the influence of contemporary and past habitat amount and fragmentation on biodiversity. Two key insights emerge from this work. First, we found that contemporary biodiversity was influenced by past landscape patterns, suggesting that birds and mammals in the Chaco respond to landscape transformation with a time delay. Second, we found evidence for time delays for most of our models including habitat fragmentation predictors, yet not for those models including habitat amount. This supports the hypothesis that time-delayed responses are

driven by habitat fragmentation and that the effects of fragmentation take time to manifest. This time delay potentially explains contrasting findings of previous fragmentation studies, and it provides a window of opportunity for conservation to avert extinctions, as species may persist in fragmented landscapes for years.

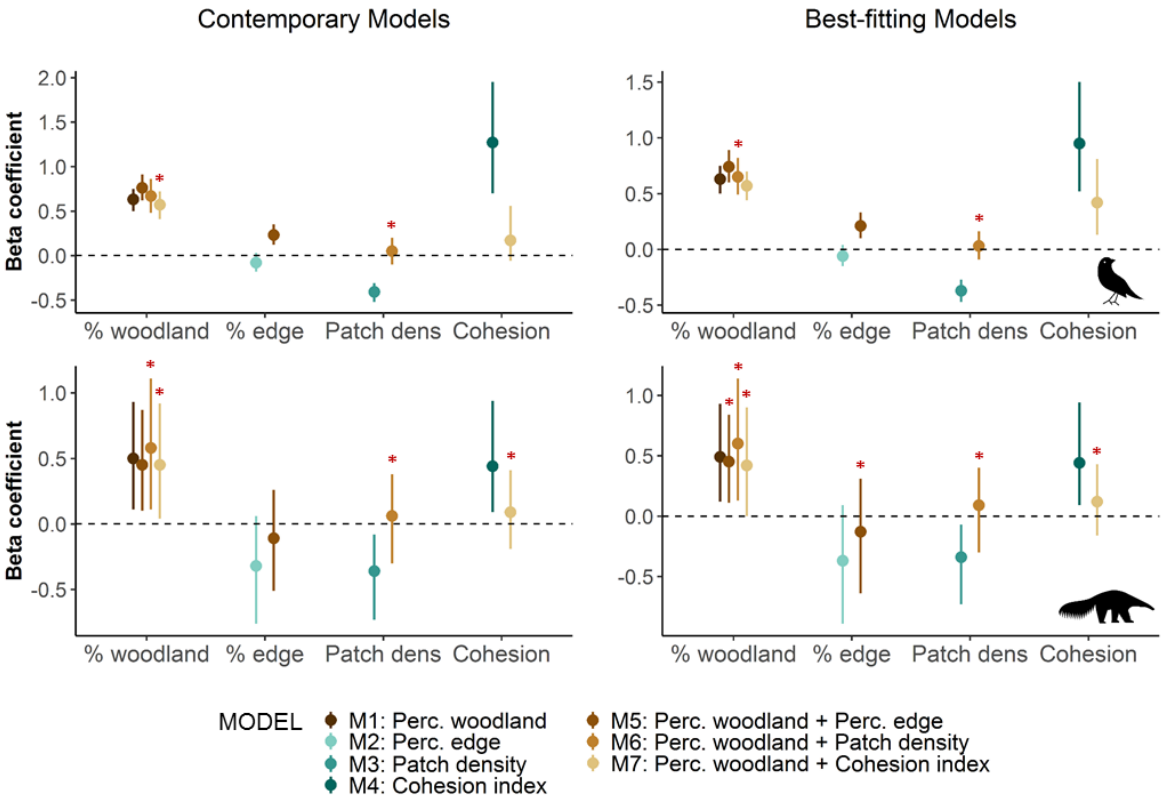


Figure III-5: Influence of landscape predictors on bird and mammal occupancyfor univariate models (habitat amount or habitat fragmentation predictors) and bivariate models (habitat amount and habitat fragmentation predictors). Plots show the standardized beta coefficients and 95% Bayesian credible intervals (95% CRI) for all predictors. The effect of a predictor on occupancy was considered to be significant when the 95% CRI did not overlap zero (dashed line). Left: beta coefficients of the contemporary models (i.e., predictors from the year of the biodiversity sampling). Right: beta coefficients of the best-fitting models (i.e., top models in Table SI III-3 and Table SI III-4). Red stars indicate that the predictor is correlated with another predictor ($r \geq 0.6$). For both taxa, the effect of *percentage of woodland* on occupancy did not vary greatly when comparing the univariate with the bivariate models. However, the effect of fragmentation differed when comparing univariate and bivariate models.

We found strong evidence that contemporary occupancy of both taxa was related to past landscape patterns, suggesting that birds and mammals have delayed responses to land-use change. Several studies have recently suggested that time-delayed effects of landscape transformation might be common, especially in regions where large-scale deforestation occurred recently (Kuussaari *et al.* 2009; Lira, de Souza Leite & Metzger 2019), such as in the Amazon (Wearn, Reuman & Ewers 2012), the Brazilian Atlantic Forest (Uezu & Metzger 2016), the Kakamega Rainforest in Kenya (Brooks, Pimm & Oyugi 1999) or the Argentine

Chaco (Semper-Pascual *et al.* 2018). Importantly, we found time-delayed responses of birds and mammals to habitat fragmentation, but not to habitat loss. This should contribute to understanding the effects of fragmentation on biodiversity, as few studies have separated the effect of habitat loss from habitat fragmentation when assessing time-delayed responses to landscape change (Krauss et al. 2010; Uezu & Metzger 2016). These studies however, relied on a few snapshots in time and were unable to estimate differences in the duration of the time-delayed response between habitat loss and habitat fragmentation (Krauss et al. 2010; Uezu & Metzger 2016; Semper-Pascual et al. 2018).

Our finding that the impacts of fragmentation can take time to manifest adds further support to evidence from long-term fragmentation experiments (Cook *et al.* 2005; Haddad *et al.* 2015) that found strongest biodiversity declines with a time delay (e.g., species richness declines across different experiments were more evident 10 years after habitat fragmentation (Haddad *et al.* 2015)). Indeed, many of the effects of fragmentation on biodiversity can take a long time to manifest. For example, changes in microclimate near forest edges lead to a gradual change in vegetation structure (Magnago *et al.* 2015), which can have knock-on effects on species' interactions (e.g., increasing nest predation risk for birds (Schneider *et al.* 2012)).

We also found interesting differences between birds and mammals regarding the estimated time-delayed response to habitat fragmentation, as this delayed response was shorter for mammals than for birds. A potential explanation for this is the high hunting pressure that mammals experience along woodland edges (Cullen Jr, Bodmer & Pádua 2000; Brashares, Arcese & Sam 2001). Rural people in the Argentine Dry Chaco prefer hunting mammals over birds (Camino *et al.* 2018). Indeed, hunting pressure increased for almost all mammal species in the Chaco in the last decades (Romero-Muñoz *et al.* 2020a). The same reason could explain why birds showed time-delayed responses to connectivity (*cohesion index*) while mammals did not: birds have a higher capacity to cross open areas compared to mammals. This is because mammals have a higher mortality risk when moving between woodland patches, as hunters often kill mammals when they cross open areas, such as agricultural fields or woodland clearings (Altrichter 2005; Semper-Pascual *et al.* 2019; Romero-Muñoz *et al.* 2020a). Together, these findings suggest that mammals may disappear faster in fragmented landscapes than birds.

Regarding the joint and individual effects of habitat amount and habitat fragmentation on biodiversity. We found that habitat amount, *percentage of woodland* in our case, was an

important predictor of bird and mammal occupancy, meaning that the resources that woodlands provide (e.g., food, refuge) are essential for both taxa. This adds further evidence to a growing number of studies that highlight the importance of habitat extent for biodiversity (Melo *et al.* 2017; De Camargo, Boucher-Lalonde & Currie 2018). Estimating the relative importance of habitat fragmentation was challenging though, as most of the fragmentation metrics were correlated with percentage of woodland. Therefore, we here only discuss the results of the models including weakly correlated ($r<0.6$) landscape predictors, as collinear predictors may give biased estimates of true effects (Ruffell, Banks-Leite & Didham 2016). Both in univariate and bivariate models, *percentage of edge* had a negative effect on mammal occupancy, again most likely due to the hunting pressure that mammals experience along woodland edges (Cullen Jr, Bodmer & Pádua 2000; Brashares, Arcese & Sam 2001). Surprisingly, however, the effect of *percentage of edge* on bird occupancy changed from negative to positive when adding *percentage of woodland* to the model (i.e., bivariate model). This suggests (i) variable interactions, (ii) a possible positive effect of fragmentation, yet also (ii) that fragmentation becomes marginally important once controlling for habitat amount (Fahrig 2013; Melo *et al.* 2017). Finally, *cohesion index* had a positive effect on bird occupancy, highlighting that forests are key for biodiversity protection in the Chaco, a finding in accordance with previous work in this region (Semper-Pascual *et al.* 2019) and other tropical deforestation frontiers (Lees & Peres 2008).

Our systematic assessment of time-delayed effects of habitat loss and fragmentation in the Chaco relied on a large biodiversity dataset, made full use of the Landsat archive to ensure consistent landscape predictors, and used occupancy models to account for imperfect detection. Still, some limitations need mentioning. First, we could not consider matrix permeability, although the type of agricultural matrix might influence species occurrence (Mastrangelo & Gavin 2014). Second, we used *patch density* to quantify the number of patches in our landscapes- including landscape metrics that capture the effect of patch size would be interesting but would require a patch-scale study (Fahrig *et al.* 2019). Finally, we built univariate models because our goal was to assess the relationship, over time, of habitat amount or habitat fragmentation on bird and mammal occupancy. Exploring the combined effect of these variables is interesting, and we therefore ran bivariate regression models by including both habitat amount and fragmentation. However, correlation between some of the landscape metrics (Figure SI III-2) suggests possible bias in the model coefficients (Ruffell, Banks-Leite & Didham 2016), and we therefore caution against over-interpreting them. An experimental approach (Haddad *et al.* 2017; Melo *et al.* 2017) or path analysis (Ruffell,

Banks-Leite & Didham 2016) would be necessary to quantify the relative importance of habitat loss vs. habitat fragmentation for time-delayed effects. Here, we limit our study to analyzing the relationship between occupancy and habitat amount over time on the one hand, and occupancy and habitat fragmentation over time on the other.

Our work has two main implications for conservation. First, our findings highlight the importance of habitat amount for birds and mammals, meaning that protection of woodland patches should be prioritized to avoid short-term local extinctions (e.g., expanding protected areas). Second, our study showed that fragmentation effects take time to manifest, resulting in a fragmentation-driven extinction debt. This provides a window of opportunity, as fragmented landscapes may still contain a high percentage of species which may otherwise go extinct if restoration activities are not implemented swiftly. Therefore, increasing landscape connectivity (e.g., restoring natural vegetation patches in the agricultural matrix) may help to prevent the loss of species vulnerable to extinction, as occupancy will keep decreasing even if no further fragmentation occurs. Additionally, to prevent local extinctions of mammals, edge effects should be diminished (e.g., expanding forested areas through active restoration actions or anti-poaching campaigns).

Our study also informs the debate on the relative importance of habitat amount vs. fragmentation. We found habitat amount to be the most important driver of contemporary biodiversity patterns. However, the effects of habitat fragmentation were also significant and, importantly, took more time to manifest. Conclusions regarding the effects of habitat fragmentation have often been based on snapshots of landscapes, typically from the time when biodiversity was sampled. Our study provides further evidence that contemporary habitat fragmentation may not be a strong predictor of species richness (Fletcher Jr *et al.* 2018), that time-delayed responses to habitat fragmentation can be strong (Haddad *et al.* 2015), and that landscape history should be considered when assessing contemporary biodiversity patterns (Kuussaari *et al.* 2009; Lira, de Souza Leite & Metzger 2019). Considering time-delayed responses seems particularly important in regions where landscapes have undergone recent and widespread changes (Lira, de Souza Leite & Metzger 2019). This is the case for many subtropical and tropical deforestation frontiers, where extinction debt due to recent landscape fragmentation is likely large and not paid in full, and a positive impact of fragmentation on overall richness might be the result. In contrast, where landscapes have been transformed long ago, extinction debt has likely been paid (Kuussaari *et al.* 2009; Lira, de Souza Leite & Metzger 2019). Overall, this suggests that land-use

history might at least explain partly the diverging conclusions from meta-analytical work on the effects of habitat fragmentation.

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Supplementary Information

Text SI III-1: Field sampling design for the birds' data.

Our bird dataset was based on three comparable, multi-year surveys, conducted between 2009 and 2014 (Mastrangelo & Gavin 2012; Macchi *et al.* 2013; Decarre 2015). All surveys relied on point counts established within 233 different sites and spread along the study area. Birds were recorded by sight or sound within a radius around each point. Bird data from Mastrangelo and Gavin (2012) was recorded in 2010 at 33 sites located in five different habitats: woodland, subsistence ranching, low intensity silvopasture, intermediate intensity silvopasture, and high intensity silvopasture. In each site, 6 points with a 25-m fixed radius were randomly located and birds were recorded during 20 minutes. Macchi *et al.* (2013) surveyed 145 sites between 2009 and 2014. Sites were located in 6 different types of habitats: woodland, subsistence ranching, silvopastures, natural grasslands, pasture plots and soybean plots. Inside each site, nine points were established in a 300 m grid. For each point count, birds were recorded during 10 minutes using a 20 m fixed radius. The bird community in Decarre (2015) dataset was sampled between 2011 and 2012 at 55 sites located in four different types of habitat: woodland, silvopastures, woodland strips and agricultural plots. Inside each site, four points were randomly selected. Points were at least 200 m apart and birds were recorded during 10 minutes per point inside a fixed radius of 100 m. Additional, detailed information regarding the field methodology is described in (Mastrangelo & Gavin 2012; Macchi *et al.* 2013; Decarre 2015).

Text SI III-2: Field sampling design for the mammals' data.

The mammalian community was characterized using data from two extensive camera-trap surveys (Decarre 2015; Gómez-Valencia 2017). In both surveys, cameras were randomly placed at each site avoiding a trail-based design where possible. The study of Decarre (2015) was carried out in 2013. In total, 101 sites were selected where camera-traps were deployed in plots located in five different types of habitat: woodland, silvopastures, woodland strips, agricultural plots and natural grasslands. Sites were randomly selected within each habitat type among a number of possible sites and a random placement strategy was used inside each plot where possible, avoiding trails and at least 300m away from the nearest edge of the habitat. Five additional sites were surveyed in 2016 following the same protocol documented in Decarre (2015). Reconyx PC800 Hyperfire Professional camera-traps were attached to trees or wooden sticks at an average height of 30cm.

The survey of Gómez-Valencia (2017) was carried out between 2014 and 2015, where 92 sites within woodlands patches of different sizes were sampled. Sampling sites were selected following the approach described in (Pasher *et al.* 2013). First, the study area was divided in a regular 1,200 ha grid, with each grid cell containing a different percent of woodland cover. Second, sites were selected depending on the accessibility and the percent of woodland cover, thus representing a wide gradient of woodland cover in the sample. Bushnell 8MP Trophy Cam HD Hybrid Trail camera-traps were placed at a height of 40-45 cm. Further detail about the camera placement and image processing is described in (Decarre 2015) and (Gómez-Valencia 2017).

Text SI III-3: Sensitivity analyses to select the radius size of the circular landscapes.

We tested three different buffer sizes for each taxon. For birds, there is no consensus on the best scale for investigating the effects of habitat change at the community level (Banks-Leite, Ewers & Metzger 2013), although a 3-km radius has been recommended to define a local landscape (Mitchell, Lancia & Gerwin 2001; Deconchat, Brockerhoff & Barbaro 2009; Mastrangelo & Gavin 2014; Semper-Pascual *et al.* 2018). Thus, we tested a 3-km radius, a smaller (2-km) and a larger (4-km) radius. For mammals, we used a 2-km radius as this size represents the average home range sizes of the woodland-dependent mammals studied (Canevari & Vaccaro 2007; IUCN 2019). We also tested a 3-km and a 4-km radius. We were unable to test a 1-km radius, as that size is too small to calculate some landscape metrics.

To select the best buffer size, we first fitted one model per buffer size and per landscape index, i.e., 12 models for each taxon (see table below). Here, we only used the landscape from the contemporary period (i.e., year of biodiversity sampling). Second, we compared the fitted models by calculating the Watanabe-Akaike information criterion (WAIC). WAIC values are provided in the table below, with numbers in bold showing the lowest WAIC value for each landscape metric and taxa.

	Birds			**Mammals**		
Landscape Metric	*2-km*	*3-km*	*4-km*	*2-km*	*3-km*	*4-km*
Contemporary % Forest	19392.74	19391.96	**19365.09**	**5659.11**	5668.50	5678.25
Contemporary % Edge	**19499.02**	19505.41	19511.78	5670.17	**5665.87**	5673.08
Contemporary Patch density	19468.59	19467.97	**19447.76**	5685.39	5676.09	**5675.54**
Contemporary Cohesion index	**19448.46**	19492.18	19534.73	**5674.94**	5684.41	5691.20

For birds, there were two buffer sizes that performed best (lowest WAIC), 2-km and 4-km radius. We thus fitted the models for the rest of the years (past landscapes) to check whether there were big differences in the results when using different buffer sizes. We found similar patterns for both buffers, and we decided to use a 4-km radius buffer as for almost all the landscape metrics, the models using a 4-km buffer performed slightly better than the models using a 2-km buffer. For mammals, for two out of the 4 landscape metrics, the models using a 2-km radius had the best fit. In addition, a 2-km radius represents the average home range sizes of the woodland-dependent mammals of our data set, and we therefore used a 2-km radius buffer for the final analyses.

Text SI III-4: Woodlan-cover maps from 1985 to 216.

We mapped annual woodland cover based on Landsat image composite metrics (hereafter: Landsat metrics), which we generated directly in Google Earth Engine using all available Landsat imagery (Gorelick *et al.* 2017). Image composites are gap-free wall-to-wall mosaics using all images from a user-defined study area in a selected time period. Metrics are statistical summaries of spectral values or indices that represent the phenological fingerprint of different land covers during that period (Frantz *et al.* 2017; Griffiths, Jakimow & Hostert 2018). For our study, we selected all available Landsat imagery for each year from 1985-2016, masked out cloud and cloud shadows, and calculated a set of in total seven metrics (i.e., mean, median, standard deviation, 10th-, 25th-, 75th- and 90th-percentile) for each of Landsat's six multispectral bands, as well as a set of spectral indices (i.e., NBR, NDMI, EVI, MSAVI and the three tasseled cap components "brightness", "greenness", "wetness"). This resulted in a total of 91 metrics for each year, which we downloaded from Google Earth Engine for further local processing.

Training data for our classification came from woodland areas (Baumann *et al.* 2017), and from forest loss polygons available for the time period 2014-2016 from GUYRA Paraguay (http://guyra.org.py/informedeforestacion). We identified our training samples by randomly sampling 1,000 points each into the "stable woodlands" and "stable non-woodlands" class, and 5,000 points across all forest loss polygons (i.e., 1,000 for each of the 5 years). We used these training points to parameterize a time-calibrated bi-annual woodland loss classification (Griffiths, Jakimow & Hostert 2018) containing three classes: (1) stable woodland, (2) stable non woodland, (3) woodland loss, and extracted the Landsat metrics for the corresponding years. For example, in case of points sampled into deforestation polygons for the year 2015, we extracted Landsat metrics for the year 2014 (i.e., pre-deforestation) and 2015 (i.e., post-deforestation), and used the same years for our stable classes. We did this for all points and all corresponding years, thereby creating a Landsat metric library independent of the specific year that than can be used for all years in a signature extension approach (Griffiths, Jakimow & Hostert 2018).

We then used these data to parameterize a random forest classifier (Breiman 2001), applied the resulting model to all bi-annual Landsat metric stacks (i.e., 1985-1986, 1986-1987, …, 2015-2016), merged these maps into a consistent map containing classes of "stable woodland", "stable other", and woodland loss for each year. Finally, we applied a minimum mapping unit of 8 pixels (i.e., ~0.7 ha) and extracted a binary woodland/other map for each year. We validated our binary maps by randomly sampling 50 points each into woodland and

non-woodland areas per year (i.e., a total of 3,100 points), examined each point individually based on the Landsat image time series (Olofsson *et al.* 2014). We followed best-practice procedures for validating each of our maps, and calculated overall accuracies as well as user's and producer's accuracies, as well as confidence intervals around these accuracies (Olofsson *et al.* 2014). All of our accuracies were corrected for possible sampling bias.

Our maps had an average accuracy of 90%, with a standard error of 0.6%. See Figure SI III-1 for overall, user's and producer's accuracies for each year.

Text SI III-5: Landscape metrics. Description of the landscape metrics used for measuring habitat amount (*percentage of woodland*) and habitat fragmentation (*percentage of edge*, *patch density* and *cohesion index*).

Percentage of woodland measures the amount of habitat in the landscape.

$$Percentage\ woodland = \frac{woodland\ pixels}{total\ pixels}$$

We also tested *percentage of core woodland* as a measure of habitat loss, however, as it was highly correlated with *percentage of woodland* (Figure SI III-2), and models based on either of these two variables were highly similar, we dropped this variable.

Percentage of edge measures the proportion of edge habitat in the landscape. We used a 30-m (1 pixel) edge width to calculate percentage. We also tested a 300-m edge since effects can extend as far as 300-400 m into the forest (Laurance *et al.* 2007; Laurance 2008). However, as models based on a 30-m edge fitted best for the mammals dataset (for birds both edges performed equally), we used the 30-m edge models.

$$Percentage\ of\ edge = \frac{edge\ pixels}{total\ pixels}$$

Patch density measures the number of patches in the landscape.

$$Patch\ density = \frac{number\ of\ woodland\ patches}{area\ buffer}$$

Cohesion index measures the structural connectedness of the patches in the landscape. The index approaches 0 as the landscape becomes increasingly subdivided and less connected (McGarigal 2014).

$$Cohesion = \left[1 - \frac{\sum_{j=1}^{n} p_{ij}^{*}}{\sum_{j=1}^{n} p_{ij}^{*}\sqrt{a_{ij}^{*}}}\right] * \left[1 - \frac{1}{\sqrt{Z}}\right]^{-1} * (100)$$

p_{ij}* = perimeter of patch ij in terms of number of pixel surfaces
a_{ij}* = area of patch ij in terms of number of pixels.
Z = total number of pixels in the buffer

Text SI III-6: JAGS code for the hierarchical multi-species occupancy model. Hierarchical multi-species occupancy model with data augmentation based on Dorazio-Royle community model with covariates (Kéry & Royle 2015).

```
model {

############### ----------------------- PRIORS  ----------------------  ###############
## Priors to describe heterogeneity among species in community (occupancy and detection)
   for (k in 1:M) {
   lpsi[k] ~ dnorm (mu.lpsi, tau.lpsi)
   betalpsi1[k] ~ dnorm (mu.betalpsi1, tau.betalpsi1)       # For % forest
   lp[k] ~ dnorm (mu.lp, tau.lp)
   betalp2[k] ~ dnorm (mu.betalp2, tau.betalp2)             # For survey (survey2)
   betalp3[k] ~ dnorm (mu.betalp3, tau.betalp3)             # For survey (survey3)
   }
## Hyperpriors to describe full community
   omega ~ dunif (0,1)                                      # Data augmentation parameter
## Occupancy model
   mu.lpsi ~ dnorm (0, 0.01)
   tau.lpsi <- pow(sd.lpsi, -2)
   sd.lpsi ~ dunif(0,5)
   mu.betalpsi1 ~ dnorm (0, 0.01)                           # % Forest covariate
   tau.betalpsi1 <- pow(sd.betalpsi1, -2)
   sd.betalpsi1 ~ dunif(0,5)
## Detection model
   mu.lp ~ dnorm (0, 0.01)
   tau.lp <- pow(sd.lp, -2)
   sd.lp ~ dunif(0,5)
   mu.betalp2 ~ dnorm (0, 0.01)                             # Survey covariate (survey2)
   tau.betalp2 <- pow(sd.betalp2, -2)
   sd.betalp2 ~ dunif(0,5)
   mu.betalp3 ~ dnorm (0, 0.01)                             # Survey covariate (survey3)
   tau.betalp3 <- pow(sd.betalp3, -2)
   sd.betalp3 ~ dunif(0,5)

############### ----------------------- MODELS  ----------------------  ###############
## Superpopulation process (w_k=1 if species k in supercommunity is available)
   for (k in 1:M) {
   w[k] ~ dbern(omega)
    }
## Ecological model for latent occurence z (z_ik=1 if species i is present at site k)
   for (k in 1:M) {
   for (i in 1:nsite) {
   logit(psi[i,k]) <- lpsi[k] + betalpsi1[k] * perc_forest[i]
   z[i,k] ~ dbern (w[k] * psi[i,k])
   }
   }
## Observational model for replicated detection/nondetection observations
   for(k in 1:M){
   for (i in 1:nsite){
   for(j in 1:nrep[i]){
   logit(p[i,j,k]) <- lp[k] + betalp2[k]* survey2[i] + betalp3[k]* survey3[i]
   Y[i,j,k] ~ dbern(z[i,k] * p[i,j,k])
   }
   }
```

```
   }

############### ----------------- DERIVED QUANTITIES ----------------- ###############
   for (i in 1:nsite){
   Nsite[i] <- sum(z[i,])                    # Number of occurring species at each site
   }
   n0 <- sum(w[(nspec+1):(nspec+nz)])        # Number of unseen species
   Ntotal <- sum(w[])                        # Total superpopualtion size

  ## For model selection
   lpsiS[1:(nspec+nz)]<- lpsi[1:(nspec+nz)]
   betalpsi1S[1:(nspec+nz)]<- betalpsi1[1:(nspec+nz)]
   lpS[1:(nspec+nz)]<- lp[1:(nspec+nz)]
   betalp2S[1:(nspec+nz)]<- betalp2[1:(nspec+nz)]
   betalp3S[1:(nspec+nz)]<- betalp3[1:(nspec+nz)]
    }
```

Text SI III-7: R code used to calculate Watanabe-Akaike information criterion (WAIC). The code is based on Broms, Hooten and Fitzpatrick (2016) and adapted for multi-species occupancy models with data augmentation.

```
## Required libraries
  library(boot)
  library(matrixStats)

## Yaug: three dimensional array (i.e., site, occasion, species) containing the detection/non-detection
## data for the observed and unobserved species
  Y2 <- aperm (Yaug,c(3,1,2))
  Yms <- Y2

## Integrate the likelihood for the whole superpopulation
  nspec <- 61
  nspec <- nspec+nz

## Saved iterations
  n.saved <- samp <- outms_model0$mcmc.info$n.samples
  tmp<-outms_ model0$sims.list
  lpsi<-array(NA,dim=c(samp,nspec))
  lp<-array(NA,dim=c(samp,nspec))
  for(i in 1:nspec){
   lpsi[,i]<-tmp$lpsiS[,i]
   betalpsi1[,i]<-tmp$betalpsi1S[,i]                    # % Forest covariate
   lp[,i]<-tmp$lpS[,i]
   betalp2[,i]<-tmp$betalp2S[,i]                        # Survey covariate (survey2)
   betalp3[,i]<-tmp$betalp3S[,i]                        # Survey covariate (survey3)
  }
  coefficients<-list(lpsi,lp)

## Derive likelihoods from JAGS output. The integrated.probs = Psi * detection.probability for each
## species, site, occasion
  derivePsiDetect <- function(coefficients,n.saved,nspec, nsite, J){
   maxSurveys <- max(J)
   psiS <- array(NA, dim=c(n.saved, nspec, nsite) )
   detectS <- array(NA, dim=c(n.saved, nspec, nsite, maxSurveys) )
   integrated.probs <- array(NA, dim=c(n.saved, nspec, nsite, maxSurveys) )

   for (i in 1:nspec) {
    for (j in 1:nsite) {
     psiS[ , i, j] <- inv.logit(lpsi[,i] + betalpsi1[,i] * cov_st$perc_forest_0yearago[j])
     for (k in 1:J[j]) {
      detectS[ , i, j, k] <-  inv.logit(lp[,i]  +
                              betalp2[,i] * cov_st$ survey2 [j] + betalp3[,i] * cov_st$ survey3[j])
          integrated.probs[ , i, j, k] <- psiS[ , i, j] * detectS[ , i, j, k]
     }}}
   return(list(psiS=psiS, detectS=detectS, integrated.probs=integrated.probs))
  }

## Likelihood value for a single species
  dmix <- function(Yms, p, psi) {
   z.tmp <- ifelse(rowSums(Yms, na.rm=T) > 0, 1, 0)
   out <- rep(0, dim(Yms)[1])    zero.idx <- (z.tmp == 0)
   out[zero.idx] <- 1 - psi[zero.idx] + psi[zero.idx] * rowProds(1 - p[zero.idx, ], na.rm=T)
```

```
  if( sum(!zero.idx) > 1) {
    out[!zero.idx] <- psi[!zero.idx] * rowProds(dbinom(Yms[!zero.idx, ], 1, p[!zero.idx, ]),
na.rm=T)
  } else{
    out[!zero.idx] <- psi[!zero.idx] * prod(dbinom(Yms[!zero.idx, ], 1, p[!zero.idx, ]), na.rm=T)
  }
  out
}

## Likelihood value for all spp, sites, MCMC
  calcLik <- function(psiS, detectS, n.saved, nsite, nspec){
    lik <- array(NA, dim=c(nspec,n.saved,nsite))
    for(i in 1:nspec){
      for(s in 1:n.saved){
        lik[i, s, ] <- dmix(Yms=Yms[i, , ],
                            p=detectS[s, i, , ],
                            psi=psiS[s, i, ])
      } }
    lik
  }

## Calculate WAIC
  waic <- function(lik, n.saved){
    meanDev <- mean(-2 * apply( log(lik), 2, sum, na.rm=TRUE ))
    (ellpd <- sum(log( apply(lik, c(1, 3), mean, na.rm=TRUE)),na.rm=TRUE))
    pd <- sum( apply( log(lik), c(1, 3), var, na.rm=T),na.rm=TRUE)
    waic <- -2*ellpd + 2 * pd
     return(list(pD=pd, waic=waic, meanDev=meanDev))
  }

  probs.out <- derivePsiDetect(coefficients=coefficients,n.saved=n.saved, nspec=nspec, nsite=nsite,
  J=J)
  out.lik <- calcLik(probs.out$psiS,probs.out$detectS, n.saved, nsite, nspec)
  waic.summary_outms_model0<- waic(out.lik, n.saved)
```

Table SI III-1: List of woodland-dependent bird species. We defined woodland-dependent species as species that inhabit areas dominated by trees and that depend on such habitat for key ecological processes (i.e., foraging, shelter and/or breeding). Such species are uncommon or absent in open habitats like savannas, grasslands, wetlands and shrublands. Bird species were categorized into woodland and non-woodland species according to expert knowledge (Macchi *et al.* 2013; Torres *et al.* 2014; Decarre 2015) and literature (Short 1975; Riogely & Tudor 1994; Del Hoyo *et al.* 2014). A total of 29 forest species were detected in our sampling sites. Species not detected during the survey but that were present in the community (8 species) were added as data augmentation in our analyses.

Scientific name	**English name**	**Detected**
Amazona aestiva	Turquoise-fronted Amazon	Yes
Asthenes baeri	Short-billed Canastero	Yes
Buteogallus coronatus	Crowned Solitary Eagle	No
Cacicus chrysopterus	Golden-winged Cacique	Yes
Campephilus leucopogon	Cream-backed Woodpecker	Yes
Campylorhamphus trochilirostris	Red-billed Scythebill	Yes
Casiornis rufus	Rufous Casiornis	Yes
Cranioleuca pyrrhophia	Stripe-crowned Spinetail	Yes
Crypturellus tataupa	Tataupa Tinamou	Yes
Cyanocorax chrysops	Plush-crested Jay	Yes
Cyclarhis gujanensis	Rufous-browed Peppershrike	Yes
Furnarius cristatus	Crested Hornero	Yes
Gampsonyx swainsonii	Pearl Kite	No
Icterus croconotus	Orange-backed Troupial	No
Icterus icterus	Venezuelan Troupial	Yes
Icterus pyrrhopterus	Variable Oriole	No
Inezia inornata	Plain Tyrannulet	Yes
Knipolegus striaticeps	Cinereous Black-tyrant	Yes
Lepidocolaptes angustirostris	Narrow-billed Woodcreeper	Yes
Leptotila verreauxi	White-tipped Dove	Yes
Megascops choliba	Tropical Screech-owl	No
Myrmorchilus strigilatus	Stripe-backed Antbird	Yes
Ortalis canicollis	Chaco Chachalaca	Yes
Pachyramphus viridis	Green-backed Becard	Yes
Piaya cayana	Common Squirrel-cuckoo	No
Piculus chrysochloros	Golden-green Woodpecker	Yes
Picumnus cirratus	White-barred Piculet	Yes
Piranga flava	Red Tanager	Yes
Pseudoseisura lophotes	Brown Cachalote	Yes
Rhinocrypta lanceolata	Crested Gallito	Yes
Setophaga pitiayumi	Tropical Parula	Yes
Spiziapteryx circumcincta	Spot-winged Falconet	Yes
Syndactyla rufosuperciliata	Buff-browed Foliage-gleaner	No
Thamnophilus caerulescens	Variable Antshrike	Yes
Thraupis sayaca	Sayaca tanager	Yes
Tiaris obscurus	Dull-colored Grassquit	No
Xiphocolaptes major	Great Rufous Woodcreeper	Yes

Table SI III-2: List of woodland-dependent mammal species. We defined woodland-dependent species as species that inhabit areas dominated by trees and that depend on such habitat for key ecological processes (i.e., foraging, shelter and/or breeding). Such species are uncommon or absent in open habitats like savannas, grasslands, wetlands and shrublands. Mammal species were classified into woodland and non-woodland species following expert recommendations (Decarre 2015; Gómez-Valencia 2017) and the literature (Canevari & Vaccaro 2007). A total of 18 forest species were detected during the camera-trap survey. Species not detected during the survey but that were present in the community (2 species) were added as data augmentation in our analyses.

Scientific name	**English name**	**Detected**
Cabassous chacoensis	Chacoan naked-tailed armadillo	Yes
Catagonus wagneri	Chacoan peccary	Yes
Cerdocyon thous	Forest fox	Yes
Dasypus novemcinctus	Nine-banded armadillo	Yes
Dolichotis salinicola	Chacoan mara	No
Eira barbara	Tayra	Yes
Leopardus geoffroyi	Geoffroy's cat	Yes
Leopardus pardalis	Ocelot	No
Mazama gouazoubira	Brown brocket deer	Yes
Myrmecophaga tridactyla	Giant anteater	Yes
Nasua nasua	South American coati	Yes
Pecari tajacu	Collared peccary	Yes
Priodontes maximus	Giant armadillo	Yes
Puma concolor	Puma	Yes
Puma yagouaroundi	Jaguarundi	Yes
Sylvilagus brasiliensis	Tapeti	Yes
Tamandua tetradactyla	Collared anteater	Yes
Tapirus terrestris	South American tapir	Yes
Tayassu pecari	White-lipped peccary	Yes
Tolypeutes matacus	Southern three-banded armadillo	Yes

Table SI III-3: Results for the bird occupancy models. Models are ranked according to the Watanabe-Akaike information criterion (WAIC). Delta WAIC (ΔWAIC) indicates the difference between the WAIC of the best model and any other model. Contemporary models are shown in bold.

PERC. WOODLAND			PERC. EDGE			PATCH DENSITY			COHESION INDEX		
Model Years ago	**WAIC**	**ΔWAIC**	**Model Years ago**	**WAIC**	**ΔWAIC**	**Model Years ago**	**WAIC**	**ΔWAIC**	**Model Years ago**	**WAIC**	**ΔWAIC**
0	**19365.09**	**0.00**	12	19463.48	0.00	4	19429.45	0.00	23	19429.8	0.00
3	19391.41	26.32	13	19466.31	2.83	1	19436.26	6.81	11	19435.65	5.85
2	19401.91	36.82	22	19486.89	23.41	2	19440.77	11.32	15	19437.56	7.76
4	19404.61	39.52	7	19487.22	23.74	**0**	**19447.76**	**18.31**	19	19441.11	11.31
1	19405.99	40.90	9	19488.22	24.74	7	19448.05	18.60	16	19446.22	16.42
6	19419.82	54.73	2	19491.17	27.70	6	19455.05	25.60	18	19447.12	17.32
7	19424.24	59.15	17	19495.84	32.37	3	19460.17	30.72	9	19450.8	21.01
5	19425.49	60.40	11	19496.44	32.97	5	19460.7	31.25	20	19452.1	22.30
11	19426.55	61.46	5	19496.48	33.01	20	19472.02	42.57	10	19452.4	22.60
15	19434.02	68.93	21	19499.58	36.10	21	19472.24	42.79	8	19453.26	23.46
17	19434.79	69.70	6	19501.93	38.45	10	19472.97	43.52	5	19453.48	23.68
8	19437.41	72.32	8	19503.21	39.73	11	19480	50.55	7	19457.22	27.42
9	19437.88	72.79	20	19504.02	40.55	9	19481.19	51.74	12	19463.86	34.06
13	19438.53	73.44	15	19504.43	40.95	16	19484.84	55.39	21	19464.03	34.23
14	19441.3	76.21	19	19505.7	42.22	23	19485.27	55.82	14	19468.25	38.45
22	19443.52	78.43	18	19506.28	42.80	14	19485.72	56.27	6	19468.42	38.62
19	19444.79	79.70	3	19508.28	44.81	17	19486.64	57.19	13	19469.84	40.04
12	19449.33	84.24	NULL	19510.72	47.24	19	19491.56	62.11	17	19473.56	43.76
10	19449.44	84.35	**0**	**19511.78**	**48.30**	15	19494.04	64.59	24	19475.18	45.38
16	19450.88	85.79	23	19513.94	50.46	8	19494.81	65.36	4	19482.94	53.14
21	19457.31	92.22	16	19515.25	51.77	24	19498.1	68.65	22	19484.34	54.54
18	19460.35	95.26	24	19517.93	54.45	18	19501.4	71.95	NULL	19510.72	80.92
24	19485.92	120.83	4	19522.22	58.75	12	19504.57	75.12	1	19526.76	96.97
23	19486.74	121.65	14	19523.48	60.01	NULL	19510.72	81.27	**0**	**19534.73**	**104.93**
20	19490.81	125.72	10	19526.91	63.44	22	19511.49	82.04	2	19535.57	105.77
NULL	19510.72	145.63	1	19534.14	70.66	13	19513.11	83.66	3	19550.36	120.56

Table SI III-4: Results for the mammal occupancy models. Models are ranked according to Watanabe-Akaike information criterion (WAIC). Delta WAIC (ΔWAIC) indicates the difference between the WAIC of the best fitting model and any other model. Contemporary models are shown in bold.

PERC. WOODLAND			PERC. EDGE			PATCH DENSITY			COHESION INDEX		
Model Years ago	**WAIC**	**ΔWAIC**	**Model Years ago**	**WAIC**	**ΔWAIC**	**Model Years ago**	**WAIC**	**ΔWAIC**	**Model Years ago**	**WAIC**	**ΔWAIC**
1	5651.43	0.00	6	5653.34	0.00	6	5684.20	0.00	**0**	**5674.94**	**0.00**
0	**5659.11**	**7.68**	7	5663.25	9.91	18	5684.27	0.07	1	5675.07	0.12
3	5659.75	8.32	9	5664.11	10.77	19	5684.57	0.37	6	5677.18	2.23
2	5662.85	11.43	4	5666.39	13.05	**0**	**5685.39**	**1.19**	2	5677.43	2.48
6	5664.96	13.53	1	5666.87	13.53	3	5685.90	1.70	3	5682.13	7.19
7	5665.95	14.52	11	5666.96	13.62	22	5688.06	3.86	4	5682.91	7.97
4	5668.43	17.00	5	5667.14	13.80	2	5688.35	4.15	5	5685.61	10.67
5	5670.52	19.09	13	5668.47	15.13	12	5688.41	4.21	8	5686.83	11.89
8	5670.91	19.48	10	5668.96	15.62	1	5688.66	4.47	7	5686.87	11.93
10	5675.52	24.10	2	5669.57	16.23	4	5688.98	4.78	9	5687.94	13.00
9	5677.15	25.72	14	5669.74	16.40	11	5689.23	5.03	11	5692.63	17.69
14	5680.25	28.82	**0**	**5670.17**	**16.83**	7	5690.86	6.66	10	5694.48	19.54
15	5680.84	29.42	8	5670.82	17.48	20	5692.77	8.58	13	5694.69	19.75
11	5683.03	31.60	15	5671.04	17.70	21	5692.93	8.73	12	5696.35	21.41
18	5685.84	34.41	3	5673.66	20.32	5	5693.69	9.49	20	5696.59	21.64
13	5686.19	34.77	12	5673.78	20.44	13	5694.09	9.89	22	5698.90	23.95
19	5686.29	34.87	19	5674.58	21.24	17	5694.15	9.96	17	5699.34	24.40
17	5687.02	35.60	16	5675.43	22.09	10	5695.00	10.80	18	5699.88	24.93
12	5687.25	35.82	24	5677.81	24.47	8	5695.07	10.88	19	5700.14	25.20
22	5692.70	41.28	23	5681.11	27.77	14	5695.91	11.71	14	5700.35	25.41
21	5693.91	42.48	17	5681.16	27.82	24	5697.76	13.56	15	5701.86	26.92
24	5694.72	43.29	21	5683.39	30.05	16	5699.40	15.20	21	5701.95	27.01
16	5694.72	43.30	22	5685.06	31.72	9	5700.33	16.13	24	5703.10	28.16
20	5696.97	45.54	18	5686.15	32.81	23	5703.03	18.83	23	5703.84	28.90
23	5701.02	49.59	20	5686.52	33.18	15	5708.39	24.19	16	5703.89	28.95
NULL	5728.61	77.18	NULL	5728.61	75.27	NULL	5728.61	44.41	NULL	5728.61	53.67

Table SI III-5: Candidate models for detection probability (*p*) for birds and mammals . Models are ranked according to Watanabe-Akaike information criterion (WAIC). Delta WAIC (ΔWAIC) indicates the difference in WAIC of the best fitting model (in bold) and any other model.

Model	Detection predictors	WAIC	ΔWAIC
	BIRDS		
DM_3	**p (Openness + Survey) ~ Ψ (1)**	**19510.72**	**0.00**
DM_1	p (Openness) ~ Ψ (1)	19838.94	328.22
DM_2	p (Survey) ~ Ψ (1)	20092.64	581.92
DM_null	p (1) ~ Ψ (1)	20620.22	1109.50
	MAMMALS		
DM_6	**p (Camera-trap + Precipitation) ~ Ψ (1)**	**5701.16**	**0.00**
DM_1	p (Camera-trap) ~ Ψ (1)	5706.33	5.17
DM_5	p (Camera-trap + Sampling effort) ~ Ψ (1)	5707.56	6.40
DM_4	p (Camera-trap + Precipitation + Sampling effort) ~ Ψ (1)	5710.70	9.54
DM_3	p (Precipitation) ~ Ψ (1)	5726.86	25.70
DM_null	p (1) ~ Ψ (1)	5728.61	27.45
DM_2	p (Sampling effort) ~ Ψ (1)	5731.44	30.29
DM_7	p (Precipitation + Sampling effort) ~ Ψ (1)	5731.63	30.47

Figure SI III-1: Overall accuracy, producer's accuracy and user's accuracy for the woodland cover maps from 1985 to 2016. Whiskers denote 95% confidence intervals around error estimates.

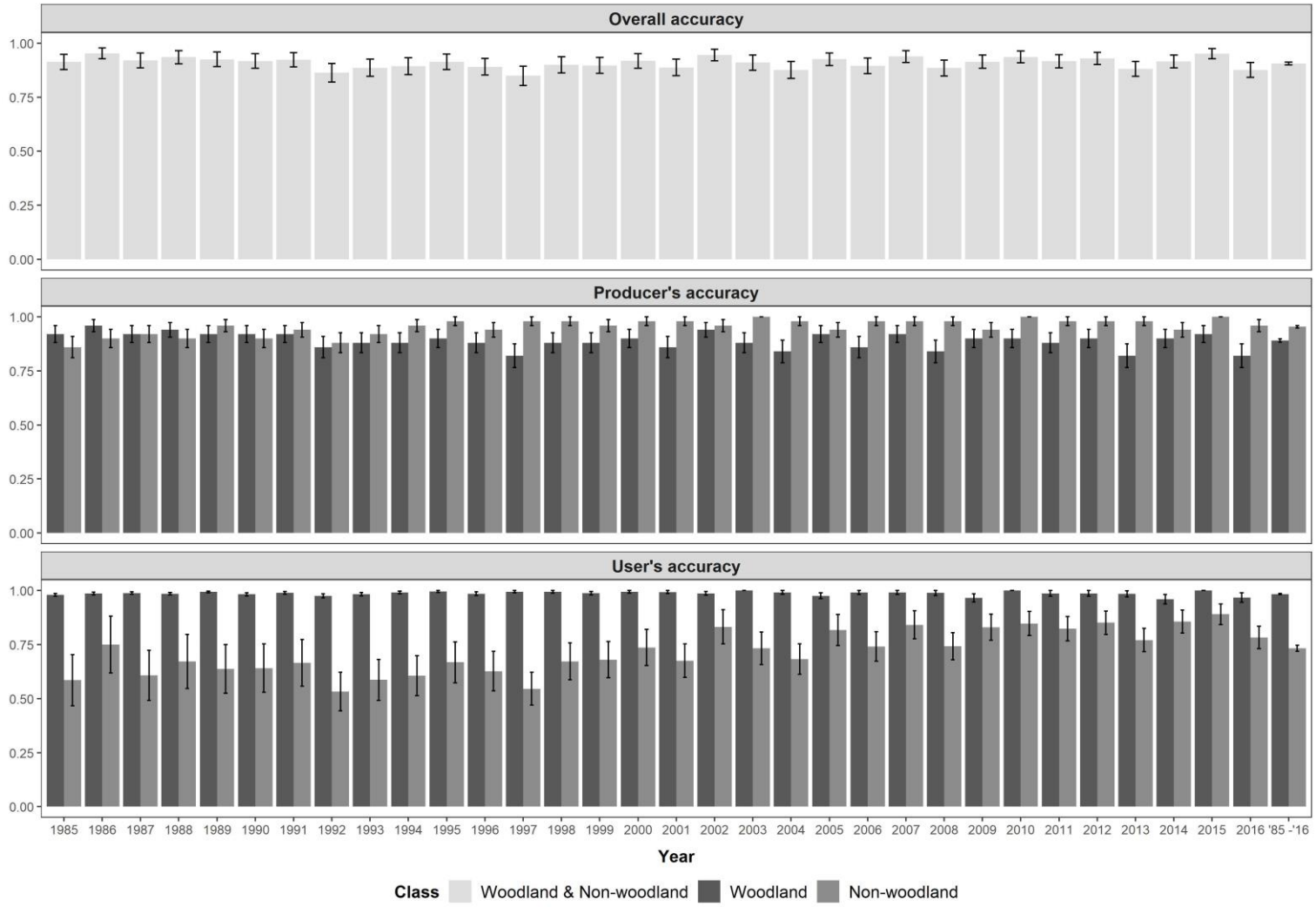
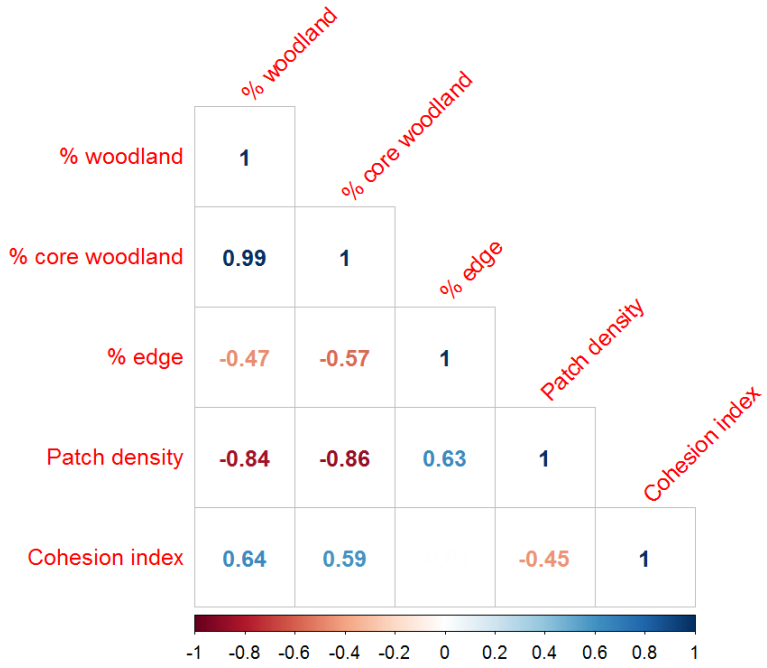


Figure SI III-2: Correlation between landscape predictors for a) birds and b) mammals. Each landscape metric includes the values for each site and each year. Positive correlations are displayed in blue and negative correlations in red. Color intensity is proportional to the Pearson's correlation coefficients annotated inside each square.

a) Birds



b) Mammals

Chapter IV:

Using occupancy models to assess the direct and indirect impacts of agricultural expansion on species' populations

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Abstract

Land-use change is a global threat to biodiversity, but how land-use change affects species beyond the direct effect of habitat loss remains poorly understood. We developed an approach to isolate and map the direct and indirect effects of agricultural expansion on species of conservation concern, using the threatened giant anteater (*Myrmecophaga tridactyla*) in the Gran Chaco as an example. We reconstructed anteater occupancy change between 1985 and 2015 by fitting single-season occupancy models with contemporary camera-trap data and backcasting the models to 1985 and 2000 land-cover/use maps. Based on this, we compared the area of forest loss (direct effect of agricultural expansion) with the area where forests remained but occupancy still declined (indirect effect of agricultural expansion). Anteater occupancy decreased substantially since 1985, particularly after 2000 when agriculture expanded rapidly. Between 1985 and 2015, ~64,000 km² of forest disappeared, yet occupancy declined across a larger area (~102,000 km²), extending far into seemingly untransformed habitat. This suggests that widespread sink habitat has emerged due to agricultural land-use change, and that species may lose their habitat through direct and indirect effects of agricultural expansion, highlighting the urgent need for broad-scale conservation planning in the Chaco. Appropriate management responses could proactively protect more habitat where populations are stable, and restore habitat or address causes of mortality in areas where declines occur. Our work also highlights how occupancy modelling combined with remote sensing can help to detect the direct and indirect effects of agricultural expansion, providing guidance for spatially targeting conservation strategies to halt extinctions.

1 Introduction

We are currently experiencing the highest extinction rates in Earth's history, mainly due to habitat destruction (Ceballos *et al.* 2015). This is particularly the case in the tropics and subtropics, where agricultural expansion and intensification are causing widespread destruction of natural vegetation (Laurance 2010). Understanding the effects of land-use change on biodiversity in these regions is therefore essential (Newbold *et al.* 2015), especially where agriculture expands into forests (Kehoe *et al.* 2017).

The most direct impact of agricultural expansion on biodiversity occurs via habitat loss and degradation. Fragmentation can also affect species directly by decreasing dispersal among patches (Hanski 2015). Additionally, indirect effects of agricultural land-use change can be observed, for instance through edge effects (Smith *et al.* 2018). This is because the accessibility of forest patches to humans increases in fragmented landscapes, and thus hunting pressure or forest fires can exert increasing pressure on species (Tabarelli, Da Silva & Gascon 2004; Corlett 2007). For example, human presence and hunting pressure are typically higher along edges of forests and protected areas (Brashares, Arcese & Sam 2001; Wittemyer *et al.* 2008). Likewise, hunting commonly occurs in or around areas where agriculture expands (Peres 2001; Romero-Muñoz *et al.* 2019; Semper-Pascual *et al.* 2019; Romero-Muñoz *et al.* 2020b). Moreover, road expansion due to agricultural expansion not only increases accessibility, but also facilitates movements by animals, thus increasing the risk of road kills (Laurance *et al.* 2006; Laurance, Goosem & Laurance 2009). Finally, habitat fragmentation also alters biophysical conditions which in turn affect species distributions (Brook, Sodhi & Bradshaw 2008). Such effects go beyond the direct conversion of habitat through agricultural expansion, but are a consequence of this land-use change. We therefore refer to such effects as indirect effects of agricultural expansion. Indirect effects are typically hard to detect and thus often overlooked, despite their importance (Brook, Sodhi & Bradshaw 2008). Approaches for identifying where and how indirect effects impact species of conservation concern are therefore needed.

Much of the work assessing the impacts of agricultural expansion on biodiversity has relied on models based on presence-only data (Gaston 2009; Guillera-Arroita *et al.* 2015), either for individual species (e.g., habitat, Romero-Muñoz *et al.* (2019)) or entire communities (e.g., richness, Ferrier and Guisan (2006)). Models based on this type of data can capture where species potentially occur, but are insensitive to detecting periods of population decline that precede local extirpation (Hobbs & Mooney 1998). Yet local extinctions can be preceded by many years of population decline (Hylander & Ehrlén 2013; Norris 2016), thus providing a

window of opportunity to prevent those losses. Unfortunately, identifying these windows of opportunity is hard, as parametrizing models that can capture population trends, such as capture-recapture models (Chandler & Royle 2013), are unfeasable or too costly for many species. Operational tools for detecting windows of opportunity preceding local extinctions are therefore often missing.

Estimating species occupancy can be a viable alternative. Occupancy is defined as the probability of a site being occupied by a species (MacKenzie *et al.* 2002), and changes in occupancy provide a robust proxy for population declines, especially useful for elusive species which are difficult to detect (Beaudrot *et al.* 2016). Yet, even though occupancy models are increasingly used in conservation (Guillera-Arroita 2017), studies typically focus on a single time period (Lindenmayer *et al.* 2012). Developing approaches which allow us to track occupancy in space and time would therefore be highly useful for mapping where population declines might be ongoing.

Furthermore, most occupancy studies assessing the impacts of agricultural expansion on biodiversity typically do not distinguish between direct and indirect effects (Gibson *et al.* 2011b; Raiter *et al.* 2014; Barlow *et al.* 2016). However, distinguishing between direct and indirect effects is crucial to spatially targeting conservation actions, in order to halt population declines of species of conservation concern. For example, proactively protecting remaining habitat from being converted should focus on areas where populations are not already declining due to anthropogenic factors (Gilroy & Edwards 2017). Conversely, other reactive conservation measures might be warranted to reduce mortality in landscapes where threatened species are in decline (e.g., anti-poaching measures, habitat restoration, corridor planning), especially if declines occur inside protected areas.

Here, we develop a new approach that backcasts occupancy models to separate the direct and indirect effects of agricultural expansion, using the Giant Anteater (*Myrmecophaga tridactyla*) (hereafter: anteater) as an example. Anteaters occur widely in Central and South America and the species is listed as vulnerable by the International Union for Conservation of Nature (IUCN) due to a ~30% population loss during the last decades (Miranda 2014). Forest is the most important vegetation type for anteaters (Di Blanco, Jiménez Pérez & Di Bitetti 2015), however, other studies have shown that they can also be associated with open habitats (e.g., grasslands or savannas; Di Blanco, Jiménez Pérez and Di Bitetti (2015), Medri and Mourão (2005)). Anteaters can also occur in anthropogenic landscapes when these landscapes provide food resources (Pardo *et al.* 2019). Although habitat loss has been proposed as a main threat to

the species (Miranda 2014), the effects of agricultural expansion on anteaters are poorly understood. To our knowledge, no study has evaluated how agricultural expansion affects anteater populations directly (e.g., through habitat conversion) and indirectly (e.g., through edge effects) anywhere in their range.

The overarching goal of our study was to estimate giant anteater occupancy in the Argentine Dry Chaco, based on contemporary camera-trap data and contemporary land-cover/use maps. We then projected this occupancy model to past land-cover/use maps from 1985 and 2000 to reconstruct anteater occupancy changes in relation to agricultural expansion. Specifically, we addressed three research questions:

1. What factors influence contemporary anteater occupancy in the Argentine Dry Chaco?
2. How did agricultural expansion influence anteater occupancy between 1985 and 2015?
3. What is the relative importance of direct versus indirect effects of agricultural expansion on anteater occupancy changes?

2 Material and methods

2.1 Study area

The Gran Chaco is the largest tropical/subtropical dry forest worldwide (1.1 million km²), extending into Argentina, Paraguay, Bolivia, and Brazil. The ecoregion is characterized by heterogeneous landscapes, with forests as the dominant land-cover (~60% of the study region), followed by open habitats such as pastures (~15%) and natural grasslands and savannas (~10%) (Baumann *et al.* 2017). Although the Chaco harbors high biodiversity (TNC *et al.* 2005), growing demand for beef and soybean have led to rapid agricultural expansion (Fehlenberg *et al.* 2017), especially after 2000. In fact, between 1985 and 2013, 20% of all forest in the Chaco was lost due to agriculture expansion for cropland (38.9% of all forest losses) or pastures (61.1% of all forest losses) (Baumann *et al.* 2017), strongly threatening biodiversity (Periago, Chillo & Ojeda 2015; Semper-Pascual *et al.* 2018).

We assessed giant anteater occupancy across the Argentine Dry Chaco. By focusing on the Dry Chaco only (i.e., excluding the Wet Chaco), we ensured that environmental conditions were fairly homogeneous across our entire study area. To delineate our specific study area, we overlaid the boundary of the Argentine Dry Chaco ecoregion with the anteater range according

to the IUCN (Figure IV-1, ~33 million ha). Our study area has a highly seasonal climate, with precipitation ranging from 450 mm to 900 mm and annual temperatures ranging between +42°C in summer to -7°C in winter (Minetti *et al.* 1999; Boletta *et al.* 2006).

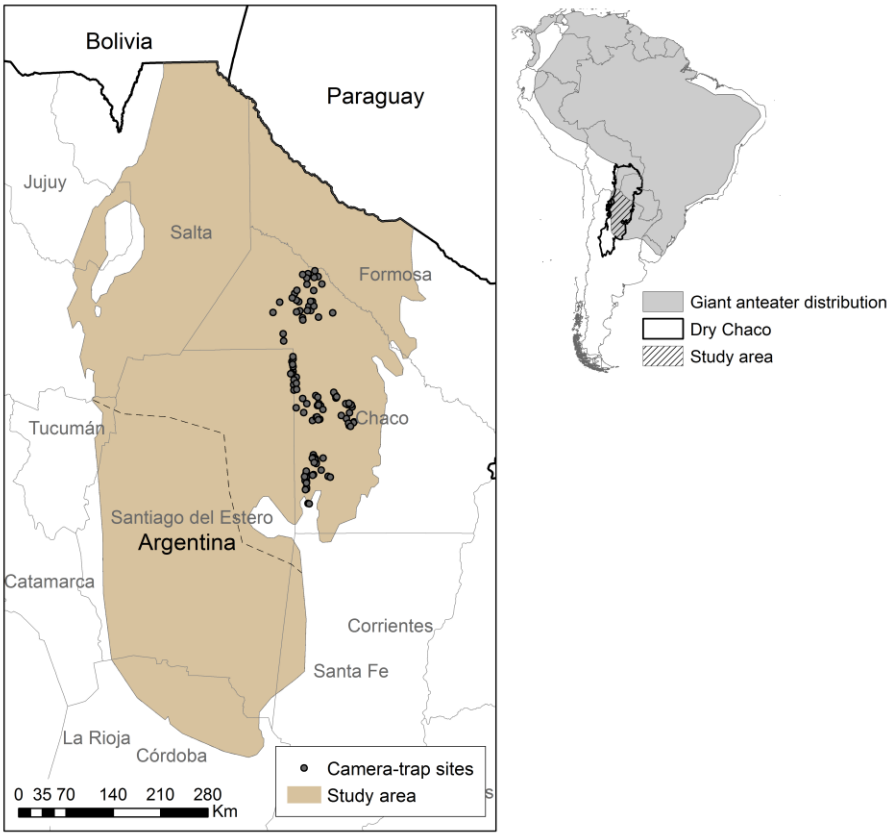

Figure IV-1: Location of the study area in South America (top-right corner map) and northern Argentina. Study area boundaries are demarcated by the overlap of the (1) Argentine Dry Chaco ecoregion boundaries with (2) anteater range according to the IUCN. Survey1 was carried out in the center of the Chaco province, survey2 in the south of the Chaco province and survey3 in the north of the Chaco province. Dotted line separates extant (north) and historic (south) giant anteater range. Names in Argentina refer to provinces.

2.2 Anteater data

We combined camera-trap data from three surveys which were all established to assess the mammal community structure in the study area: the first survey (survey1) was carried out in 2013 (Decarre 2015), the second survey (survey2) in 2014-2015 (Gómez-Valencia 2017) and the last survey (survey3) in 2016-2017 (Proyecto Quimilero). Camera-trap sites were distributed across the extant range of the species (northern part of the study area, Figure IV-1). We did not sample the southern part of the study area, as according to the current IUCN range map, anteaters are absent there (Miranda 2014). Sites were selected randomly while avoiding trails, to sample the full diversity of vegetation types in the region, and to avoid bias due to high capture rates along trails (Wearn *et al.* 2013; Kolowski & Forrester 2017). In addition,

such a sampling design has been recommended for estimating occupancy (Wearn *et al.* 2013; Burton *et al.* 2015). Camera-trap sites were separated by at least 1,500 m from one another, a distance approximately representing the radius of an average circular anteater home range (Table SI IV-1). Further details on the camera placement are provided in Text SI IV-1.

2.3 Predictor variables

We used four variables for modelling anteater detection probability: *camera-trap survey*, *sampling effort*, *temperature*, and *precipitation* (Table IV-1 and Table SI IV-2). For occupancy probability, we selected four landscape variables known to influence anteater habitat selection: *percentage of forest cover*, *percentage of open habitats*, *percentage of edge* between forest and open habitats, and a *diversity index* of suitable habitats (i.e., forest and open habitats) (Table IV-1 and Table SI IV-2). Importantly, these variables by themselves are not measures of direct or indirect effects of agricultural expansion.

The entire range of each landscape variable was represented by our camera-traps (Figure SI IV-1). Given that camera-trap data were collected during different years, we used two high-resolution (30 m) land-cover/use maps to relate each camera-trap site to the corresponding land-cover/use map. We therefore related the camera-trap sites from survey1 to a land-cover/use map from 2013 (Baumann *et al.* 2017) and the camera-trap sites from survey2 and survey3 to an updated land-cover/use map from 2015 consistent with Baumann *et al.* (2017) (Figure SI IV-2). We thus parametrized one single model. Such a modelling approach (i.e., time-calibrated model) is widely used and has several advantages compared to models based on data from a single time period (Nogués-Bravo 2009; Kuemmerle *et al.* 2012; Sieber *et al.* 2015; Romero-Muñoz *et al.* 2019). Time-calibrated models use all available data to parameterize a single model not linked to a specific time period, to then project this model into different time periods (Nogués-Bravo 2009). Consequently, time-calibrated models describe species' niches more fully, are less prone to sampling bias and ensure that observed changes are solely due to changes in predictor variables (and not due to different model parameterizations) (Nogués-Bravo 2009; Kuemmerle *et al.* 2012). The latter is particularly important in the context of our goal to separate the direct from the indirect effects of agricultural expansion.

To derive landscape indices, we used Morphological Spatial Pattern Analysis (Vogt *et al.* 2007) and Shannon's diversity index (McGarigal 2014) and summarized them using a 1,500 m radius circular moving window. We also tested a larger radius, however, as models based on variables

for the 1,500 m circular radius fitted best and align with home range estimates, we only show these results. In addition to the landscape variables, we included three variables reflecting human disturbance: *distance to settlements*, *distance to roads*, and *distance to paved roads* (Table IV-1 and Table SI IV-2). Importantly, all these human-disturbance indicators were time-invariant (i.e., they were calculated using data from ~2015), as we assumed that expansion of main roads or settlements did not greatly affect the region during the study period (Romero-Muñoz *et al.* 2020a).

Table IV-1: Variables for estimating anteater detection probability and occupancy probability. Variables are based on Desbiez and Medri (2010), Di Blanco *et al.* (2017), Di Blanco, Jiménez Pérez and Di Bitetti (2015) and Medri and Mourão (2005).

Variable	Description	Hypothesis
	DETECTION	
Survey	Camera-trap survey	Different study designs could lead to different detection probabilities
Effort	Number of days that the camera-traps were active	The probability of detecting individuals should be higher with increasing survey effort
Temp[a]	Mean temperature of the month when the cameras were active	Anteaters are less active during extreme temperatures (i.e., too hot or cold)
Prec[a]	Mean precipitation of the month when the cameras were active and the month before	During the dry season, anteaters walk longer distances to find water and probability of detection should increase
	OCCUPANCY	
Landscape structure (measured within a 1,500 m radius from the cell)		
Forest	Percentage of forest	Anteaters use woody vegetation to shelter and rest. Forests also provide microclimates to help regulate body temperature
OpenHabitat[b]	Percentage of open habitat (grasslands, savannas and pastures)	Anteaters use grasslands and savannas for foraging
Edge	Percentage of pixels located between forest and open habitat patches	Anteaters prefer areas where food resources and refuges are in close proximity
Diversity[b]	Shannon's diversity index considering only suitable land-use classes (forest, grasslands, savannas and pastures) (McGarigal 2014)	Anteaters prefer heterogeneous landscapes where they can find areas for both resting and feeding
Human Disturbance		
Sett	Euclidean distance to the closest settlement	Anteaters avoid areas with high human pressure
Roads	Euclidean distance to the closest road (both paved and non-paved)	Roads are an indicator of disturbance (e.g., providing access for hunters)
PavRoads[b]	Euclidean distance to the closest paved road	Paved roads are accessible after heavy rains contrary to non-paved roads and human disturbance is expected to be more persistent

[a] Correlated variables ($r \geq 0.6$) that were not included in the same detection model

[b] Correlated variables ($r \geq 0.6$) removed from the final dataset for modelling occupancy. Since forest is considered essential habitat for the species ((Di Blanco, Jiménez Pérez & Di Bitetti 2015)), when two variables were correlated we retained the one including forest (i.e., forest and edge)

We aggregated all variables to a 300 m pixel resolution, using an equal-area coordinate system. This pixel resolution is much smaller than the average anteater home range (~9 km2, Table SI IV-1). We standardized all variables (0 = mean, 1 = standard deviation) and checked for collinearity. When two variables were correlated (Spearman correlation coefficient ≥ 0.6), we retained the ecologically more meaningful variable (Table IV-1).

2.4 Modeling anteater occupancy

We used a likelihood-based, single-season occupancy model (MacKenzie *et al.* 2017) to estimate anteater occupancy (Ψ) in relation to landscape and human disturbance variables, while accounting for detectability (p). During wildlife surveys, individuals are often unobserved, either because they are truly absent at the sampling site, or because they are present, but undetected. Visiting each sampling site on multiple occasions enables the estimation of detection probability, which can be incorporated into the occupancy modelling to correct for imperfect detection (MacKenzie *et al.* 2002).

We generated sampling occasions by pooling daily detection/non-detection records for each sampling site into consecutive camera-days. We carried out sensitivity analyses to check for differences in occupancy and detection estimates when pooling daily detection/non-detection records into different number of camera-days. We defined an occasion as an interval of seven camera-days (see Figure SI IV-3). We only included sites that were actively surveyed for more than 21 consecutive days to obtain a minimum of three occasions per site, and a maximum of 84 days (i.e., 12 occasions) to account for the closure assumption of occupancy models. Therefore, we estimated true occupancy as we assumed that changes in occupancy between occasions did not occur. The number of occasions per site ranged between 3 and 12 (mean = 6.1) with a sampling effort per site ranging from 21 to 84 days (mean = 43). The final sample included a total of 106 camera-trap sites.

Occupancy models link a state model determining occupancy at each site with an observation model for detection which is conditional on occupancy. We first modelled detection probability and then occupancy probability. To model detection probability, we only included detection variables, using a null occupancy model. We considered all possible combinations of variables, while excluding correlated variables in the same model, and tested a quadratic effect of temperature as we hypothesized that anteater detection is lower during extreme temperatures. We ranked the resulting models using Akaike's Information Criterion, corrected for small

sample size (AICc; Burnham and Anderson (2002)), where the detection model with the lowest AICc is best-fitting.

To model occupancy probability, we kept the best-fitting detection model constant and included variables that could affect anteater occupancy. We excluded correlated variables (see Table IV-1) and built six candidate models (Table IV-2). Given that habitat loss is the main threat to anteaters (Miranda 2014), we built a first set of candidate models testing all possible combinations of landscape structure variables. In addition, to test whether human disturbance may affect anteater occupancy, we built a second set of candidate models in which we included human disturbance variables to the models from the first set (Table IV-2). We compared all resulting models, ranked them according to AICc and considered models with a ΔAICc < 2 to be competing. We used model averaging by calculating weighted average estimates based on models with ΔAICc < 2 and following Burnham and Anderson (2002). To assess model fit, we ran a goodness-of-fit test on the global model and calculated an overdispersion parameter ($\hat{c}$) (MacKenzie and Bailey 2004), using 10,000 bootstrap replicates and the Pearson $\chi 2$ statistics. We fitted our models using the R package *unmarked* (Fiske & Chandler 2011).

2.5 Mapping changes in anteater occupancy over time

To map changes in anteater occupancy over time, we used our single-season, time-calibrated model to predict anteater occupancy for the years 2015, 2000, and 1985. The year 2015 represents the average year of our sampling period and the most recent land-cover/use map for our study area. The year 2000 marks the beginning of the period when land conversion drastically increased. Finally, 1985 marks a baseline before this wave of conversion and fine-scale satellite images are available for land-use classifications.

Our approach relied on several assumptions. First, we assumed that the relationship between anteater occupancy and landscape variables remained unchanged over the study period, meaning that factors describing contemporary anteater occupancy would also describe past anteater occupancy. Second, land-cover/use variables were the only time-variant variables in our models as we assumed that no major changes in terms of roads/settlements expansion occurred during the study period. Finally, agricultural expansion is the dominant process leading to change in land-cover. Therefore, if our models find differences in anteater occupancy across time, we assume that these differences can only arise from effects of agricultural expansion on our predictor variables.

To predict current anteater occupancy across our study area, we used model-averaged estimates derived from our time-calibrated occupancy model and the land-cover/use map from 2015. We then backcasted anteater occupancy by projecting the same model to the past land-cover/use maps from 1985 and 2000 (Figure SI IV-2). Habitat models have been widely used to predict habitat across larger regions, as well as to reconstruct past habitat (Varela, Rodríguez & Lobo 2009; Tapia *et al.* 2018). Predictions are considered to be reliable when they are made within the range of environmental conditions used for model building, in our case the contemporary data (Elith & Leathwick 2009). To ensure we predicted to similar environmental conditions as those represented by our data, we compared the distributions of predictor variables at the camera-trap sites with the overall distribution of the predictor variables for the study area and for each time period we assessed (Figure SI IV-4 and Figure SI IV-5). This showed that even though we projected our models across large areas in space and back in time, we did not predict anteater occupancy to areas with environmental conditions not represented by the data used to calibrate our models. In other words, while we projected our models to large areas, we did not extrapolate.

To estimate changes in anteater occupancy over time, we calculated the difference in occupancy predictions for each 300 m pixel between (1) 1985-2000 (i.e., occupancy predictions in 2000 minus occupancy predictions in 1985), (2) 2000-2015, and (3) 1985-2015. We assessed the uncertainty of the resulting predictions using a parametric bootstrap procedure (Davison & Hinkley 1997) with 10,000 replications. Further details on the uncertainty assessment are provided in Figure SI IV-6.

To assess the relative importance of direct versus indirect effects of agricultural expansion on occupancy, we compared the area in which occupancy declined with the area directly affected by forest loss due to agricultural expansion (i.e., conversion from forest to cropland and pasture). We only considered conversions from forest to cropland and pasture, not conversions of other habitats such as grasslands and savannas, since forest is considered essential habitat for the species (Mourão & Medri 2007; Di Blanco, Jiménez Pérez & Di Bitetti 2015), and as other land uses are not widespread in the study area. We refer to the direct effect of agricultural expansion as those areas where forest was converted. An indirect effect of agricultural expansion occurs in those areas where occupancy declined yet forests were stable during the observation period (Figure IV-2). In these areas, a decrease in anteater occupancy can only be attributed to indirect effects of agricultural expansion (e.g., increase of human pressure along forest edges or expansion of logging-trails).

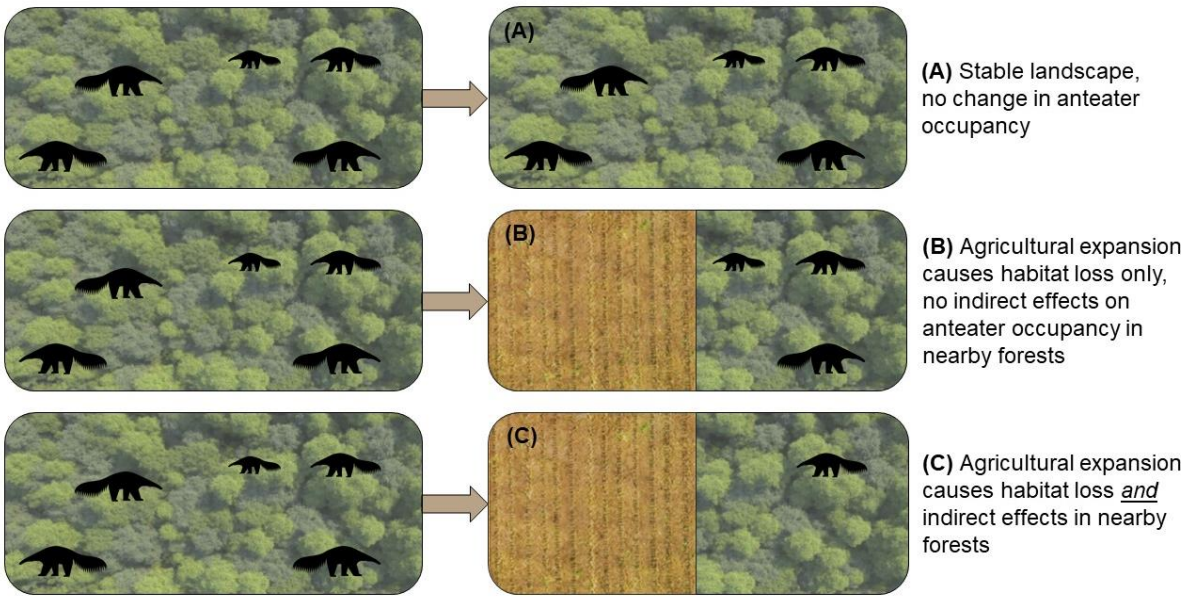

Figure IV-2: Direct and indirect effects of agricultural expansion on anteater occupancy. Agricultural expansion affects anteater population declines directly where forest is converted to croplands or pastures. However, anteater population declines can additionally occur in nearby forests via indirect effects of agricultural expansion, for example due to the expansion of roads, heavier traffic, easier access for hunters, or fires escaping from agricultural land. In our model, such effects collectively lead to declining anteater occupancy in otherwise stable forests.

3 Results

Our dataset contained 71 independent anteater captures over 4,508 trap-days (mean capture rate = 1.57 captures/100 trap-days). The naïve occupancy (i.e., proportion of sites with at least one detection) was 42%. Our best-fitting detection model contained the variables *survey* and *temperature* (Table IV-2), indicating that detection probability varied among the three camera-trap surveys and that it increased slightly with increasing temperature. The estimated detection probability across all sites was 0.14 (SE = 0.03).

The landscape variable *percentage of forest* had the strongest influence on occupancy probability and was selected in all three top models (ΔAICc <2). The best-fitting model included only *percentage of forest* (Table IV-2). The second-best model also included *percentage of edge*, and the third-best model additionally included *distance to roads* and *settlements*. Model-averaged coefficients also corroborated that *percentage of forest* was the most important variable, with a positive effect on anteater occupancy (Table IV-3 and Figure SI IV-7). *Percentage of edge* had also a positive effect on occupancy, but weaker than percentage of forest (Table IV-3). Regarding the human disturbance variables, occupancy probability increased further away from *settlements*, but decreased with *distance to roads*

(Table IV-3). The goodness-of-fit test on the global model indicated that our model fitted the field data well (p-value = 0.95) and that the data were not overdispersed ($\hat{c}$ = 0.05).

Table IV-2: Candidate models ranked by AICc. The first part of the table lists the detection models (best-fitting model in bold), the second part shows the occupancy models (models with ΔAICc <2 in bold). Akaike weights (AICcw) quantifies the probability of each model being the best model.

Model	Variables	AICc	ΔAICc	$AICc_w$
	DETECTION			
M_11	**p (Temp + Survey) ~ Ψ (1)**	**379.19**	**0.00**	**0.47**
M_9	p (Temp + Effort + Survey) ~ Ψ (1)	381.43	2.24	0.15
M_6	p (Temp + I(Temp^2) + Survey) ~ Ψ (1)	381.44	2.25	0.15
M_3	p (Survey) ~ Ψ (1)	382.69	3.50	0.08
M_4	p (Temp + I(Temp^2) + Effort + Survey) ~ Ψ (1)	383.73	4.53	0.05
M_7	p (Effort + Survey) ~ Ψ (1)	384.21	5.02	0.04
M_15	p (Prec + Survey) ~ Ψ (1)	384.21	5.02	0.04
M_13	p (Prec + Effort + Survey) ~ Ψ (1)	385.81	6.61	0.02
M_1	p (Effort) ~ Ψ (1)	391.57	12.37	0.00
M_14	p (Prec + Effort) ~ Ψ (1)	393.34	14.15	0.00
M_10	p (Temp + Effort) ~ Ψ (1)	393.55	14.35	0.00
M_5	p (Temp + I(Temp^2) + Effort) ~ Ψ (1)	394.66	15.47	0.00
M_2	p (Temp + I(Temp^2)) ~ Ψ (1)	402.88	23.68	0.00
M_Null	p (1) ~ Ψ (1)	403.04	23.85	0.00
M_12	p (Prec) ~ Ψ (1)	403.88	24.69	0.00
M_8	p (Temp) ~ Ψ (1)	404.15	24.96	0.00
	OCCUPANCY			
M_1	**p (Temp+Survey) ~ Ψ (Forest)**	**375.10**	**0.00**	**0.43**
M_3	**p (Temp+Survey) ~ Ψ (Forest + Edge)**	**375.86**	**0.76**	**0.29**
M_4	**p (Temp+Survey) ~ Ψ (Forest + Roads + Sett)**	**376.96**	**1.87**	**0.17**
M_6	p (Temp+ Survey) ~ Ψ (Forest + Edge + Roads + Sett)	379.35	4.25	0.05
M_5	p (Temp+ Survey) ~ Ψ (Edge + Roads + Sett)	379.91	4.81	0.04
M_2	p (Temp+ Survey) ~ Ψ (Edge)	380.72	5.62	0.03
M_Null	p (1) ~ Ψ (1)	403.04	27.94	0.00

Table IV-3: Coefficient estimates (± SE) for the top three models and the model average. All variables are standardized to 0 mean and 1 standard deviation for comparison.

	DETECTION				OCCUPANCY				
						Landscape		Human Disturbance	
	p(Int)	*p(Temp)*	*p(Survey1)*	*p(Survey3)*	*Ψ(Int)*	*Ψ(Forest)*	*Ψ(Edge)*	*Ψ(Roads)*	*Ψ(Sett)*
M_1	-1.80±0.28	0.32±0.19	0.74±0.37	-1.78±0.49	1.88±1.36	1.40±0.99			
M_3	-1.84±0.25	0.29±0.18	0.63±0.34	-1.76±0.48	3.36±1.61	1.97±1.08	1.63±1.30		
M_4	-1.74±0.27	0.36±0.19	0.79±0.37	-1.80±0.50	1.56±0.74	0.91±0.59		-0.14±0.70	0.90±0.60
Avg.	-1.80±0.27	0.32±0.19	0.71±0.36	-1.78±0.49	2.30±1.55	1.50±1.03	0.54±1.07	-0.03±0.31	0.17±0.44

Occupancy maps highlighted that areas with a high percentage of forest cover had the highest occupancy probabilities, while agricultural areas had the lowest occupancy probabilities (Figure IV-3 and Figure SI IV-2). Areas with high occupancy values were more extensive in 1985 than in 2000, and experienced an even greater decline in area between 2000 and 2015 (Figure IV-3). The mean estimated occupancy across 10,000 pixels randomly selected from the study area was 84.59% (SE = 13.23) in 1985 and 72.90% (SE = 16.18) in 2015.

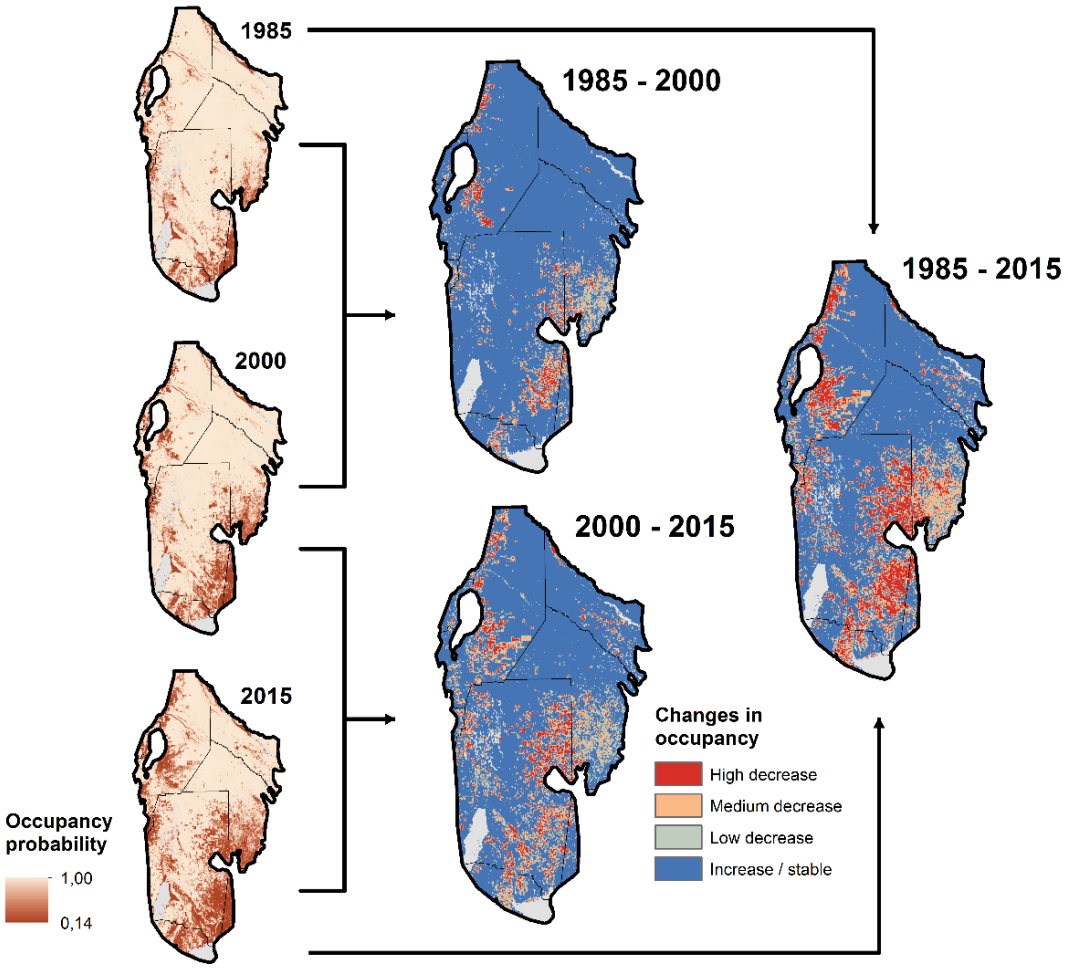

Figure IV-3: Predicted anteater occupancy for the years 1985, 2000 and 2015 (left column) and changes in anteater occupancy between (1) 1985 and 2000, (2) 2000 and 2015, and (3) 1985 and 2015 (right columns). The maps of changes in occupancy show four categories: (a) increase/stable where occupancy has increased (between 6-35%) or stayed stable (change ≤6%), (b) low decrease (between 6-19%), (c) medium decrease (between 19-46%), and (d) high decrease (between 46-84%). Permanent water bodies are depicted as light gray.

Estimated occupancy changes for individual pixels ranged from -84% to +35%. We classified occupancy changes into four categories based on quartiles (Figure SI IV-8): (a) increase/stable occupancy where occupancy increased (increase of 6-35%) or stayed stable (increase or decrease up to 6%), (b) low decrease (6-19% decrease), (c) medium decrease (19-46% decrease), and (d) high decrease (46-84% decrease). High decreases in occupancy mainly

occurred in agricultural areas (e.g., agricultural frontiers in the Chaco and Santiago del Estero provinces). Conversions to cropland typically resulted in highest occupancy decreases, whereas lower decreases were seen for conversions to pasture (Figure SI IV-9). Areas where occupancy stayed stable or increased were widespread in 1985-2000, but became scarce in 2000-2015. The same was true for the 1985-2015 period, suggesting that anteater occupancy decreased especially after 2000. Only areas characterized by a high share of forest cover (e.g., the El Impenetrable region in the north of Chaco province or the Copo National Park in the north-east of Santiago del Estero province) had increasing or stable occupancy at the end of our study period (Figure IV-3). The uncertainty assessment of our occupancy change map based on parametric bootstrapping indicated that the standard deviation of our predictions of occupancy change was +/-8.39% (Figure SI IV-6).

To separate the direct and indirect effects of agricultural expansion, we compared the area of forest loss with the area where anteater occupancy declined in our study region. Anteater occupancy decreased over wide areas and these areas were much more extensive than the area directly affected by forest loss. Decrease in anteater occupancy occurred over approximately 102,000 km^2 (31% of the study region, Figure IV-4). In contrast, only 64,000 km^2 (20% of the study region) experienced forest conversion to agriculture, with 34,000 km² being converted to pastures and 30,000 km² to croplands (Figure IV-4).

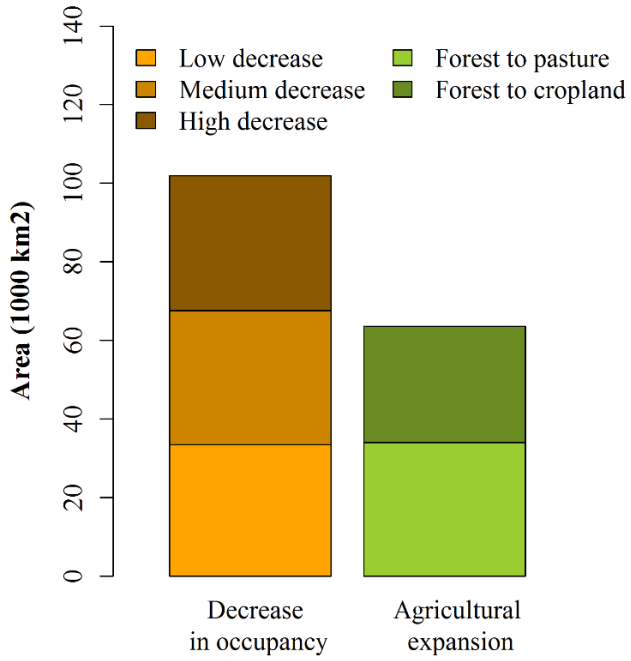

Figure IV-4: Decrease in anteater occupancy (low, medium and high) versus agricultural expansion (forest conversion to cropland and to pastures).

4 Discussion

Agricultural expansion in the tropics is a major cause of local extinctions. Focusing on anteaters in the Argentine Dry Chaco, we demonstrate how projecting a time-calibrated occupancy model back in time can reconstruct occupancy change and separate the direct and indirect effects of agricultural expansion on species of conservation concern. Forest cover was the main driver of anteater occupancy, and consequently, the widespread deforestation driven by agricultural expansion in the Chaco has led to drastic declines in anteater occupancy, with only a relatively small proportion of the study area characterized by stable or increasing occupancy in 2015. Most areas turning from stable to declining occupancy did so after 2000, when landscape transformation increased. Importantly, anteater occupancy declined over much wider areas than those directly affected by forest loss, and occupancy declines extended far into seemingly untransformed habitat. This suggests that agricultural expansion has substantial and widespread indirect effects on species of conservation concern – beyond the spatial footprint of agricultural expansion itself. Stopping the decline of anteaters and other large mammals in the Chaco will thus require swift conservation action and planning, and our study can help to target both proactive and reactive management interventions to tackle ongoing defaunation. More broadly, we show how relatively simple and broadly applicable tools can help to provide a spatial template for conservation planning to mitigate the direct and indirect impacts of agricultural expansion.

Anteater occupancy was primarily affected by landscape variables, especially forest cover, and occupancy increased with forest cover. This aligns with prior research emphasizing the value of forest for anteaters (Di Blanco, Jiménez Pérez & Di Bitetti 2015), and is reasonable given that forests provide refuge from predation and protect from extreme temperatures. Edges between forest and open habitats were also positively related to anteater occupancy, however, edges had a lower effect on occupancy than did forest. One possible explanation is that anteaters usually rest in forested areas, and use open habitats for feeding and for moving between forest patches (Medri & Mourão 2005; Desbiez & Medri 2010).

We found that anteaters avoided areas close to human settlements, but selected areas close to roads, a finding in line with other studies (Vynne *et al.* 2011; Di Blanco, Jiménez Pérez & Di Bitetti 2015; Quiroga *et al.* 2016). Although vehicle collisions have been proposed as a main cause of anteater mortality (Miranda 2014), anteaters are known to use roads to move through agricultural landscapes (Vynne *et al.* 2011), and our results suggest that they do not perceive roads as a threat. Additionally, anteaters in the Chaco are rarely hunted by people (Altrichter

2006; Camino *et al.* 2018) and this may explain why roads, a proxy for accessibility for hunters, did not negatively affect anteater occupancy in our case. The avoidance of human settlements can be explained by the widespread presence of dogs, which can attack and kill anteaters (Lacerda, Tomas & Marinho-Filho 2009). However, the effects of presence of dogs and humans on anteaters in the Argentine Dry Chaco were still less important than the effects of forest cover (Table SI IV-3).

Our predictions showed that much of the Argentine Dry Chaco still has a high probability of anteater occupancy, especially in the north. In contrast, the south has less potential habitat, and the species is locally extinct there. The high occupancy estimates in the north of our study area can be explained by a combination of three factors: relatively large remaining forest patches, low hunting pressure on anteaters (Altrichter 2006; Camino *et al.* 2018), and the absence or extremely low density of jaguars, the anteaters' main predator (Astete, Sollmann & Silveira 2008; McBride, Giordano & Ballard 2010; Sollmann *et al.* 2013), in the study area (Quiroga *et al.* 2014; Romero-Muñoz *et al.* 2019).

Although our models predicted relatively high occupancy in areas with high forest cover, our occupancy change maps first and foremost showed a drastic decrease in occupancy due to forest loss driven by agricultural expansion. In areas where agriculture expanded, occupancy decreased by up to 84% between 1985 and 2015, especially after 2000, when deforestation rates in the Chaco soared due to technological innovations in agriculture (e.g., introduction of genetically modified soybean), rising global soybean prices, and government incentives to foster agricultural expansion (Goldfarb & Zoomers 2013; Baumann *et al.* 2017; Fehlenberg *et al.* 2017). Areas with increasing or stable occupancy were relatively widespread during the first period, but became scarce after 2000 and are now limited to remote areas with high forest cover. Few such areas remain in the Chaco. Some of these consist of larger protected areas (Figure SI IV-10), yet others remain beyond the current agricultural frontier. Factors explaining why agriculture has not expanded in these areas include the presence of indigenous communities, the national zoning plan that prohibits deforestation in some areas, and low market access from such regions (Piquer-Rodríguez *et al.* 2018).

In the Chaco, anteater occupancy decreased over an area almost twice as large as the area affected by forest loss (i.e., anteater occupancy decreased across and area of ~102,000 km² and forest loss occurred on an area of ~64,000 km²). This suggests that agricultural expansion not only directly affects anteater occupancy via habitat conversion, but also has strong indirect effects that contribute to population declines beyond the footprint of forest conversion. For

example, agricultural expansion typically leads to improvements of infrastructure and therefore, an increase in traffic, which in turn increases road mortality (Cáceres *et al.* 2010). Similarly, where agriculture expands, an inflow of people can occur, and pets and humans have easier access to previously remote areas. Additionally, agricultural expansion and associated human accessibility is increasing fire frequency in the Chaco (Argañaraz *et al.* 2015), and such fires are considered to be a key threat for the species (Miranda 2014). Finally, forest loss alters local and regional climate (Brook, Sodhi & Bradshaw 2008), leading to drier and hotter conditions, which in turn amplify fire risk (Argañaraz *et al.* 2015). These potentially strong indirect effects that exceed far beyond the actual agricultural footprint are in line with findings from other regions though few studies have assessed this. For instance, extinction rates reported from West Africa were higher than those predicted by species-area models, likely due to hunting pressure along reserve edges (Brashares, Arcese & Sam 2001). Similarly, accessibility and hunting pressure increased due to forest fragmentation in tropical Asian forests (Corlett 2007). Our study provides further empirical evidence for the strong synergistic effects of land-use change and other extinction drivers.

Land-cover/use variables were the only time-variant predictors included in our models. This allowed us to reveal that the indirect impact of agricultural expansion on occupancy can extend far into seemingly untransformed habitats. Three alternative explanations for occupancy declines in untransformed habitat are possible, but not plausible for anteaters in the Chaco: (1) other environmental changes, (2) hunting pressure, and (3) time-delayed effects. Regarding other environmental changes, climate change might impact anteater occupancy. However, the Argentine Dry Chaco has neither experienced marked changes in climate during our study period (Figure SI IV-11), nor is the Chaco a climatically marginal area for anteaters, as anteaters occupy both drier and wetter areas today (Miranda 2014). Hunting pressure has increased in the Chaco over the last decades (Romero-Muñoz *et al.* 2019), likely due to improved road infrastructure, population increase, and the decline of forested areas. However, as mentioned above, anteaters are not targeted by hunters. We are not aware of any variable not related to, and driven by, agricultural expansion that might plausibly explain the broad-scale declines in anteater occupancy.

The third alternative explanation for anteater declines in untransformed habitats is time-delayed effects of habitat loss (Brook, Sodhi & Bradshaw 2008; Semper-Pascual *et al.* 2018). A time-delayed response would mean that historical landscape patterns (e.g., from 2000 or 1985) explain contemporary occupancy patterns better than current landscape patterns (Kuussaari *et*

al. 2009). We tested for this and found that current occupancy patterns were best explained by current landscape patterns (Table SI IV-4), suggesting no major time-delayed effect after habitat conversion. Yet occupancy in areas where agriculture expanded recently (i.e., 2000-2015), was higher than occupancy in areas where agriculture expanded longer ago (i.e., 1985-2000) (Figure SI IV-12), possibly because the strength of indirect effects of agricultural expansion on anteaters wanes over time.

We used a large camera-trap dataset and our occupancy framework resulted in robust models and plausible occupancy patterns. Still, some uncertainties remain. First, we used a time-calibrated model that ensures observed changes in occupancy are solely due to changes in predictor variables, and that makes full use of all available camera-trap data (Nogués-Bravo 2009). Estimating occupancy based on past anteater data would have been interesting, but no dataset that would allow this analysis exists. Second, some predictor variables did not have a strong effect on anteater occupancy, and there was considerable uncertainty surrounding the effect of these predictors (Table IV-3). Yet, the goodness-of-fit test indicated that our models fitted the field data adequately, and the estimated errors of our spatial predictions were small, together suggesting that our inferences were robust. This suggests robust model projections, which form the basis for our separation of direct and indirect effects of agricultural expansion (rather than directly interpreting model coefficients). Third, we predicted occupancy over a large geographic extent and back in time. These predictions were made to areas within the range of environments sampled by our camera-trap sites, and thus we did not extrapolate (Figure SI IV-4 and Figure SI IV-5), but we cannot fully exclude non-stationarity in the relationship between anteater occupancy and variables. Fourth, we interpreted our occupancy estimates as a proxy for population change. A high correlation between occupancy and abundance estimates has been previously demonstrated for several species (Clare, Anderson & MacFarland 2015; Linden *et al.* 2017; Parsons *et al.* 2017), however, this correlation remains untested for anteaters in the Chaco. Finally, detection probability differed among the three camera-trap surveys. We controlled for this by (1) including the variable survey in our detection model, and (2) relating each observation to the site-specific environmental variables from the sampling period. Still, a more homogenized survey design (e.g., same camera-trap brand) would have been preferable.

Overall, our results provide further evidence of the impacts of agricultural expansion on biodiversity. The fact that anteaters, a species which can tolerate certain levels of anthropogenic disturbance (Quiroga *et al.* 2016), may be greatly affected by forest loss, suggests that the

consequences of agricultural expansion may be even more drastic for strictly forest-dependent species. Identifying the effects of forest conversion on biodiversity is therefore crucial for conserving anteaters and many other species. Our results showed that besides the direct effects of agricultural expansion, indirect effects are widespread. Identifying these often-overlooked indirect effects is therefore crucial but also challenging, as they can go unnoticed in forests that seem untransformed. In such forests, however, other threats such as hunting and forest fires can exert a major pressure on wildlife (Redford 1992; Brook, Sodhi & Bradshaw 2008; Benítez-López *et al.* 2017). As the footprint of agriculture expands in many tropical areas, paying closer attention to the additional and larger footprint of indirect negative impacts on wildlife becomes crucial.

Methodologically, we demonstrated how projecting time-calibrated occupancy models over time may help to identify the indirect effects of agricultural expansion, and to separate areas affected by direct versus indirect effects. Such a spatially-explicit approach can be used to predict occupancy declines, and thus can potentially reveal population declines before critical thresholds are reached. More generally, understanding and mapping occupancy declines due to direct and indirect effects of agricultural expansion provides starting points for conservation planning and for targeting conservation action. Proactive conservation strategies (e.g., protecting remaining core habitat) should be targeted in areas where occupancy increases or remains stable, and reactive strategies (e.g., restoring sink habitat) in areas where declines are occurring due to direct forest conversion. Additionally, to counteract the indirect effects of agricultural expansion, conservation actions should focus on implementing measures to lessen such indirect effects, for example through fire regulation, especially in areas that seem untransformed but where species' declines are observed.

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Supplementary Information

Text SI IV-1: Camera trapping.

We used data from three independent camera-trap surveys:

Survey1 (Decarre 2015) was carried out between August 2013 and December 2013 in the central part of the Chaco province. A 10 x 10 km grid was placed over a map of that area (100 x 60 km), ten grid-cells were randomly selected and inside each grid-cell, a stratification of 5 different land-uses was made. For our analyses, 48 sites were included where camera-traps were deployed in plots or patches of homogeneous habitat: forest (15), forest strips (13), natural grasslands (3), silvopasture (8) and agriculture (9). Habitat patches inside the grid-cell and sites inside each habitat were randomly selected and at least 300m apart from the edge of the habitat. Reconyx PC800 Hyperfire Professional Camera-traps were attached to trees or wooden sticks at an average height of 30 cm.

Survey2 (Gómez-Valencia 2017) was carried out between December 2014 and September 2015 in the southern part of the Chaco province, an area highly affected by agricultural expansion. In this area, 28 sites within forest fragments of different sizes were included. The sampling sites were selected following Pasher *et al.* (2013). First, the study area was divided in a regular 1,200 ha grid, with each grid cell containing a different percent of forest cover. Second, sites were selected depending on the accessibility, and the percent of forest cover, thus representing a wide gradient of forest cover in the sample. Bushnell 8MP Trophy Cam HD Hybrid Trail camera-traps were placed at a height of 40-45 cm.

Survey3 (Proyecto Quimilero) was carried out between October 2016 and May 2017 in the northern part of the Chaco province, an area that contains continuous and well-preserved forest patches. 30 sites were included in forest and shrubland habitats. Sites were randomly selected in a 6,000 km^2 study area, trying to avoid trails and separated at least 6,000 m from one another. Bushnell Strike Force HD camera-traps were placed at an average high of 25 cm.

Further detail about the camera placement and images processing of the two first surveys is described in Decarre (2015) and Gómez-Valencia (2017).

Table SI IV-1: Reported home range sizes of giant anteaters

Home Range (km^2)	**Reference**
3.00	Canevari and Vaccaro (2007)
9.00	Canevari and Vaccaro (2007)
5.70	Medri and Mourão (2005)
11.90	Medri and Mourão (2005)
9.00	Silveira *et al.* (1999)
25.00	Montgomery and Lubin (1977)
3.70	Shaw, Machado-Neto and Carter (1987)
2.70	Shaw, Machado-Neto and Carter (1987)
8.75	AVERAGE

Table SI IV-2: Variables and data sources used to predict anteater occupancy for 2015, 2000 and 1985.

Variables by group	Name	Data Sources		
		2015	2000	1985
DETECTION				
Temperature*	Temp	INTA weather stations (http://siga2.inta.gov.ar)	-	-
Precipitation*	Prec		-	-
OCCUPANCY				
Landscape structure				
Extent of forest	Forest	Baumann *et al.* (2017) This study	This study	This study
Extent of open habitats	OpenHabitat			
Extent of edge between forest and open habitats	Edge			
Diversity index	Diversity			
Human Disturbance				
Distance to settlements	Sett	www.indec.gob.ar	-	-
Distance to roads	Road	www.ign.gob.ar; Dirección de Vialidad Provincial (DVP) – Chaco	-	-
Distance to paved roads	PavRoad	www.ign.gob.ar	-	-

* Argentine National Institute of Agrarian Technologies (INTA) weather stations consist of point data. We interpolated the point data to obtain continuous maps for our study area using Kriging.

Table SI IV-3: Candidate models including the models used to test the effects of humans and dogs on anteater occupancy. The predictor Humans/Dogs contains the presence of humans and/or dogs at each camera-trap site. The table includes AICc, ΔAICc and model weights (AICcw) for all the candidate models. Models are ranked by AICc and models with ΔAICc <2 are shown in bold.

Model	Variables	AICc	ΔAICc	AICcw
M_1	**p (Temp + Survey) ~ Ψ (Forest)**	**375.10**	**0.00**	**0.37**
M_3	**p (Temp + Survey) ~ Ψ (Forest + Edge)**	**375.86**	**0.76**	**0.25**
M_4	**p (Temp +Survey) ~ Ψ (Forest + Roads + Sett)**	**376.96**	**1.87**	**0.15**
M_7	p (Temp + Survey) ~ Ψ (Forest + Roads + Sett + Humans/Dogs)	378.85	3.76	0.06
M_Null	p (Temp + Survey) ~ Ψ (1)	379.19	4.10	0.05
M_6	p (Temp + Survey) ~ Ψ (Forest + Edge + Roads + Sett)	379.35	4.25	0.04
M_5	p (Temp + Survey) ~ Ψ (Edge + Roads + Sett)	379.91	4.81	0.03
M_2	p (Temp + Survey) ~ Ψ (Edge)	380.72	5.62	0.02
M_8	p (Temp + Survey) ~ Ψ (Forest + Edge + Roads + Sett + Humans/Dogs)	381.19	6.09	0.02
M_9	p (Temp + Survey) ~ Ψ (Edge + Roads + Sett + Humans/Dogs)	382.28	7.18	0.01

p: probability of detection
Ψ: probability of occupancy

Table SI IV-4: Models used to test for time-delayed responses to land-use changes. The table includes AICc, ΔAICc and model weights ($AICc_w$) for all the candidate models. Models were built using contemporary anteater data as response variable and 1) present (2015) and 2) past (2000 and 1985) landscape structure variables as predictors. Models are ranked by AICc. Models including contemporary landscape structure variables (i.e., year 2015) fit better than models including past landscape structure variables, meaning that anteaters may not be affected by extinction debt.

Model	Variables	AICc	ΔAICc	$AICc_w$
M_1_2015	p (Temp+Survey) ~ Ψ (Forest $_{2015}$)	375.10	0.00	0.25
M_3_2015	p (Temp+Survey) ~ Ψ (Forest $_{2015}$ + Edge $_{2015}$)	375.86	0.76	0.17
M_1_2000	p (Temp+Survey) ~ Ψ (Forest $_{2000}$)	376.69	1.59	0.11
M_4_2015	p (Temp+Survey) ~ Ψ (Forest $_{2015}$ + Roads + Sett)	376.96	1.87	0.10
M_4_2000	p (Temp+Survey) ~ Ψ (Forest $_{2000}$ + Roads + Sett)	378.08	2.99	0.06
M_5_2000	p (Temp+ Survey) ~ Ψ (Edge $_{2015}$ + Roads + Sett)	378.22	3.12	0.05
M_4_1985	p (Temp+Survey) ~ Ψ (Forest $_{1985}$ + Roads + Sett)	378.66	3.56	0.04
M_3_2000	p (Temp+Survey) ~ Ψ (Forest $_{2000}$ + Edge $_{2000}$)	378.93	3.83	0.04
M_6_2015	p (Temp+ Survey) ~ Ψ (Forest $_{2015}$ + Edge $_{2015}$ + Roads + Sett)	379.35	4.25	0.03
M_6_2000	p (Temp+ Survey) ~ Ψ (Forest $_{2000}$ + Edge $_{2000}$ + Roads + Sett)	379.73	4.63	0.02
M_5_1985	p (Temp+ Survey) ~ Ψ (Edge $_{1985}$ + Roads + Sett)	379.86	4.76	0.02
M_5_2015	p (Temp+ Survey) ~ Ψ (Edge $_{2015}$ + Roads + Sett)	379.91	4.81	0.02
M_2_2000	p (Temp+ Survey) ~ Ψ (Edge $_{2000}$)	380.25	5.15	0.02
M_6_1985	p (Temp+ Survey) ~ Ψ (Forest $_{1985}$ + Edge $_{1985}$ + Roads + Sett)	380.41	5.31	0.02
M_2_2015	p (Temp+ Survey) ~ Ψ (Edge $_{2015}$)	380.72	5.62	0.02
M_2_1985	p (Temp+ Survey) ~ Ψ (Edge $_{1985}$)	380.98	5.89	0.01
M_1_1985	p (Temp+Survey) ~ Ψ (Forest $_{1985}$)	381.44	6.34	0.01
M_3_1985	p (Temp+Survey) ~ Ψ (Forest $_{1985}$ + Edge $_{1985}$)	383.04	7.94	0.00
M_Null	p (1) ~ Ψ (1)	403.04	27.94	0.00

p: probability of detection
Ψ: probability of occupancy

Figure SI IV-1: Density plots for our time-variant predictors. The plots include percentage of edge and percentage of forest, showing the distribution of predictor values at the location where camera-traps were deployed (between 2013 and 2017) and the distribution of predictor values for the entire study area in 1985, 2000 and 2015. The plots show that the distribution of values at the camera-trap locations covers the entire range of values represented in our study area. In terms of sampling frequency, our sample of camera trap locations did contain lower frequencies of sites with a low percentage of forest than were available in the landscape. However, as anteaters are absent from entirely open landscapes in the Chaco, this did not bias our occupancy models.

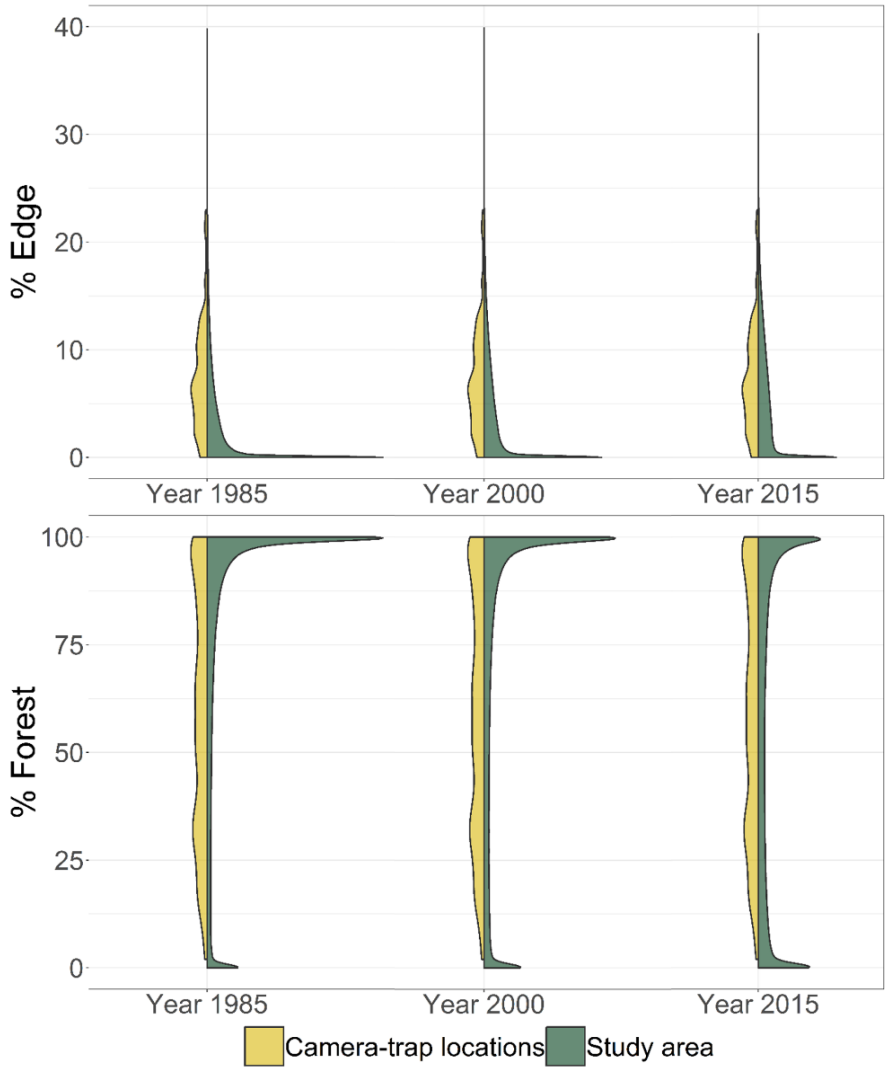


Figure SI IV-2: Land-cover maps for the years 1985, 2000 and 2015 Maps have a resolution of 30 meters and were created following the methodology documented in Baumann *et al.* (2017).

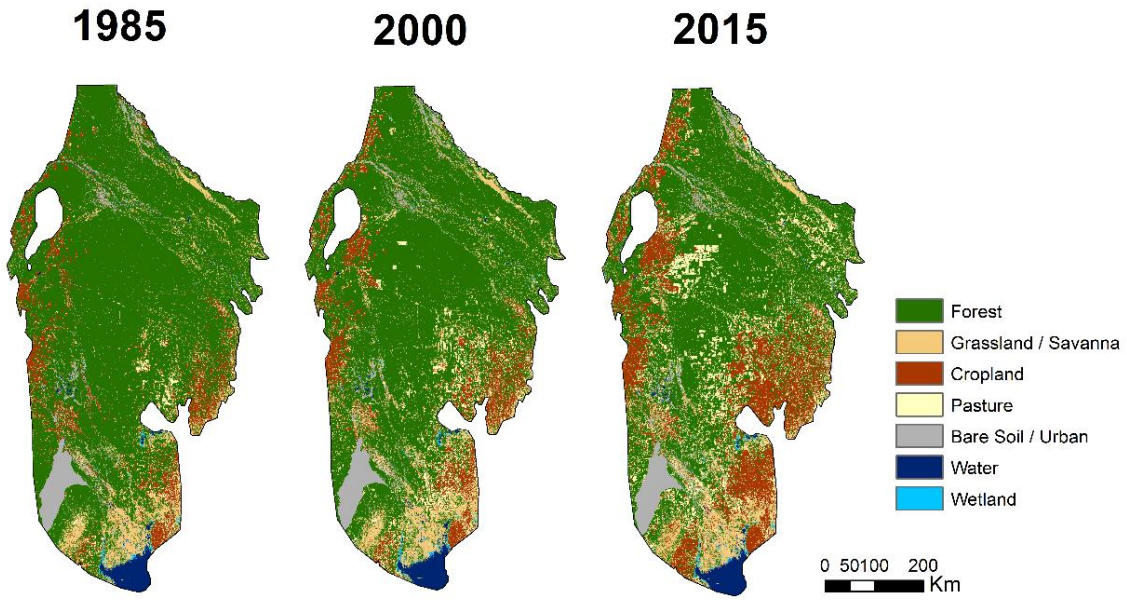


Figure SI IV-3: Occupancy and detection estimates for different sampling intervals. Estimates include 95% confidence intervals for the null model and for different sampling intervals (from 4 to 10-day occasions). Both occupancy and detection estimates typically increase with the number of days per occasion. 7-day occasions were used to strike a balance between high detection estimates and small confidence intervals.

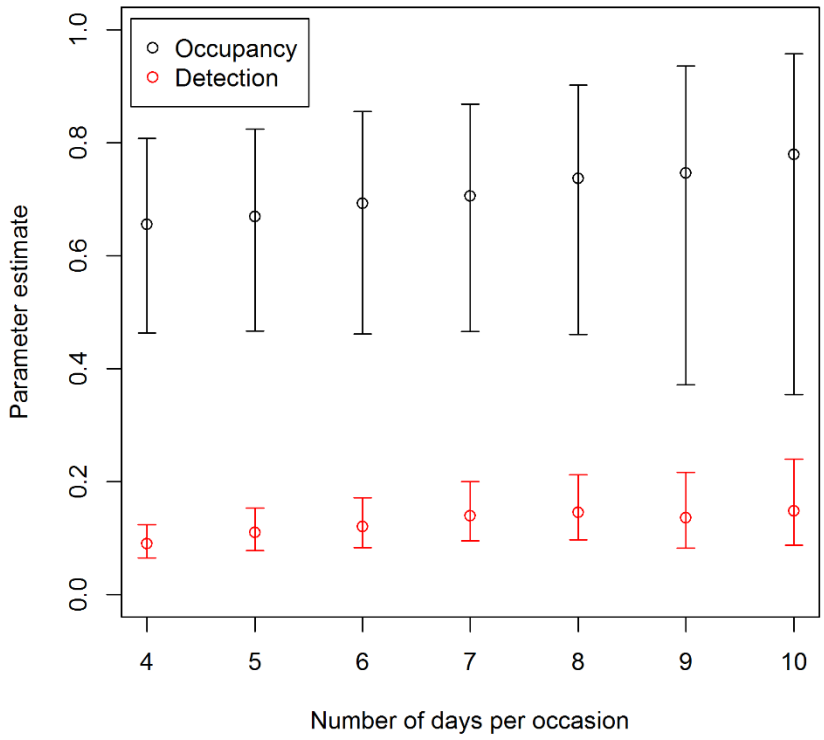
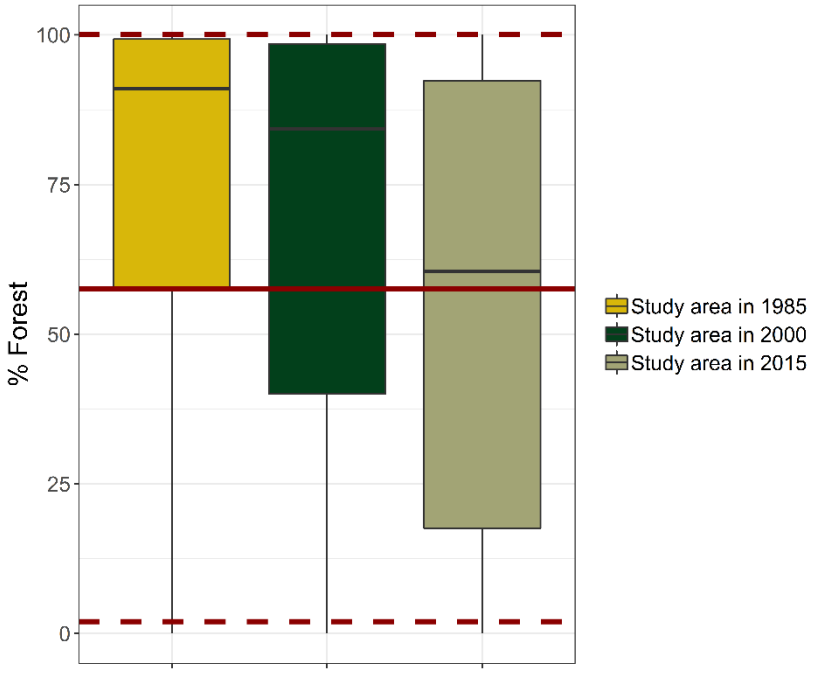


Figure SI IV-4: Distribution of values of our time-variant predictors for the entire study area in 2015, 2000 and 1985. Red horizontal line represents the median value of the camera-trap locations. Red horizontal dashed lines represent the maximum and minimum values of the camera-trap locations. The plots show that (1) the median of the pixel values of the study area in 2015 (i.e., approximately when the surveys took place) aligns very well with the median of the values of the camera-trap sites, and (2) the minimum and maximum (excluding outliers) pixel values of the study area for the three time periods are within the minimum and maximum values of the camera-trap sites.



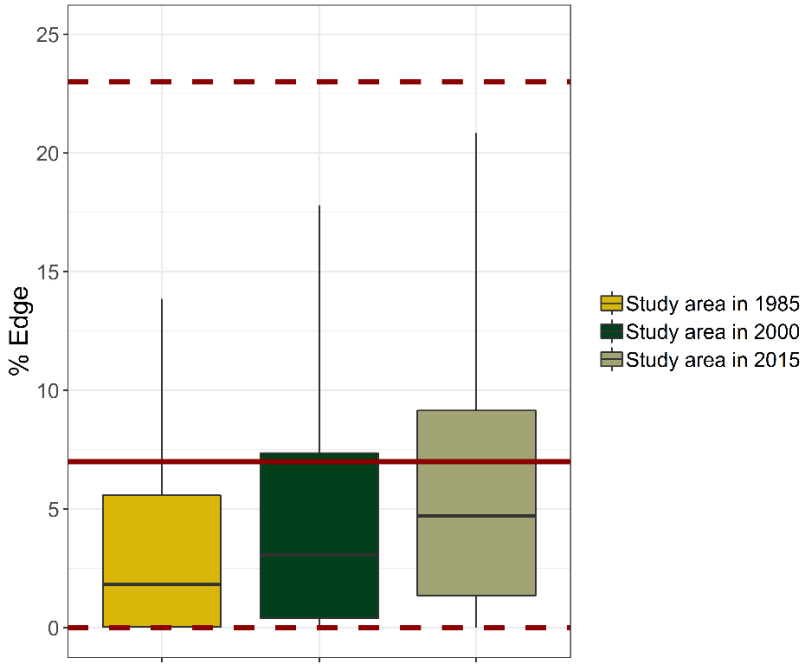


Figure SI IV-5: Distribution of values of our time-invariant predictors for the whole study area. Red horizontal line represents the median value of the camera-trap locations. Red horizontal dashed lines represent the maximum and minimum values of the camera-trap locations. The plot shows that (1) the median of the pixel values of the study area in 2015 (i.e., approximately when the surveys took place) aligns well with the median of the values of the camera-trap sites, and (2) the minimum and maximum (excluding outliers) pixel values of the study area are within the minimum and maximum values of the camera-trap sites.

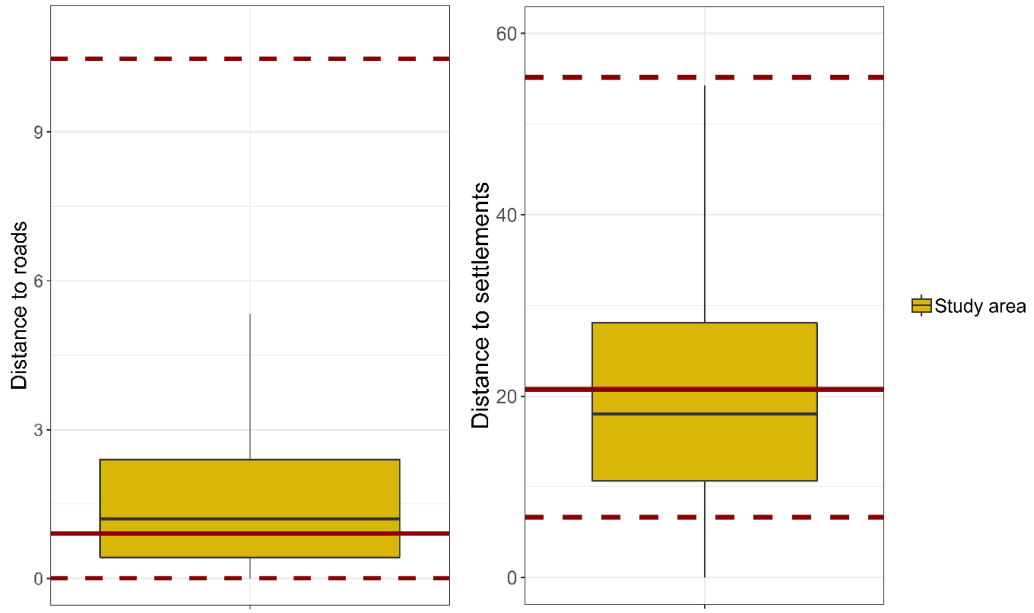


Figure SI IV-6: Distribution of occupancy change between 1985 and 2015 obtained from 10,000 bootstrap replications. To assess the uncertainty of our predicted changes in anteater occupancy, we used a parametric bootstrap procedure (Davison & Hinkley 1997). We randomly generated 10,000 bootstrap replications of predictions, based on the estimated model parameters and their uncertainty. For each bootstrap replication, we estimated the mean occupancy in 1985 and in 2015. Finally, we quantified the variation in occupancy change between 1985 – 2015 across 10,000 replications. This yielded a standard deviation of +/- 8.39%. The distribution of the mean changes in occupancy obtained from the 10,000 bootstrap replications is shown below.

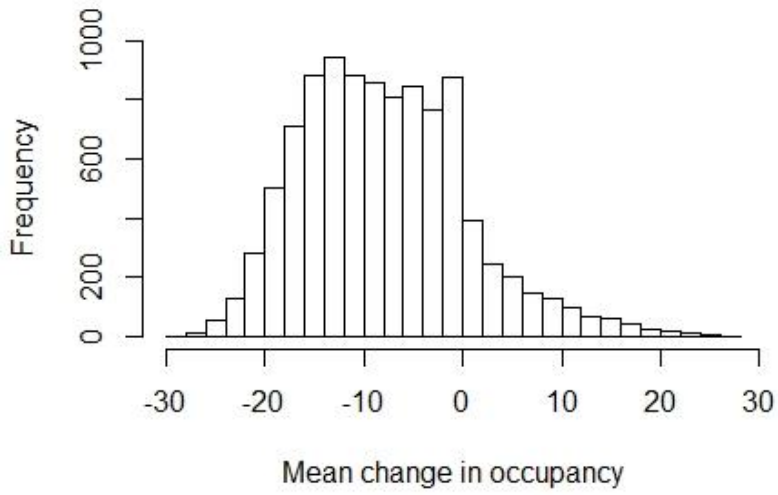


Figure SI IV-7: Correlation between anteater occupancy probability and percentage of forest coverfor the model with averaged coefficients. Light gray lines represent the 95% confidence interval.

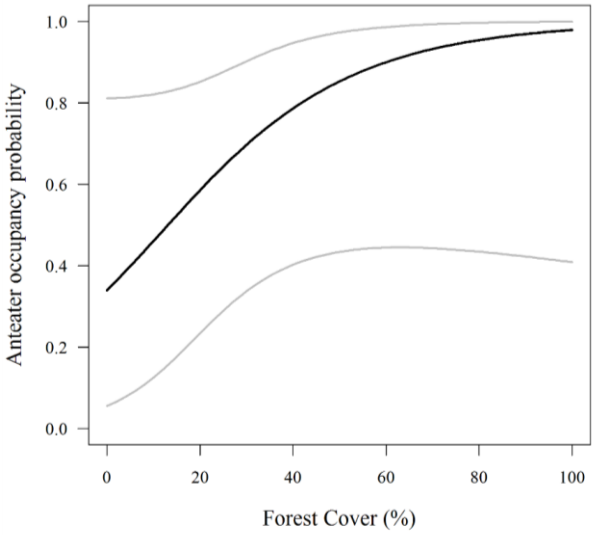


Figure SI IV-8: Distribution of occupancy change between 1985 and 2015. Histograms show the distribution of the changes in occupancy values across the study region and the median for a) all the pixel values, b) negative values (decrease in occupancy) and c) positive values (increase in occupancy). To define *stable occupancy*, we calculated the median of the distribution of negative values (i.e., decrease in occupancy, median = -6%) since occupancy declines are most relevant from a conservation point of view. We therefore defined as stable occupancy those pixels where there was a change in occupancy (positive or negative) ≤6%. We then subdivided the negative values smaller than the median (-6% to -84%) into three quantiles (each including one third of the observations) to obtain the categories *low decrease* (occupancy declines 6-19%), *medium decrease* (decrease 19-46%), and *high decrease* (decrease 46-84%). Increasing values above 6% were assigned to the class *increase*. Note that occupancy decreases >84% did not occur in the landscape.

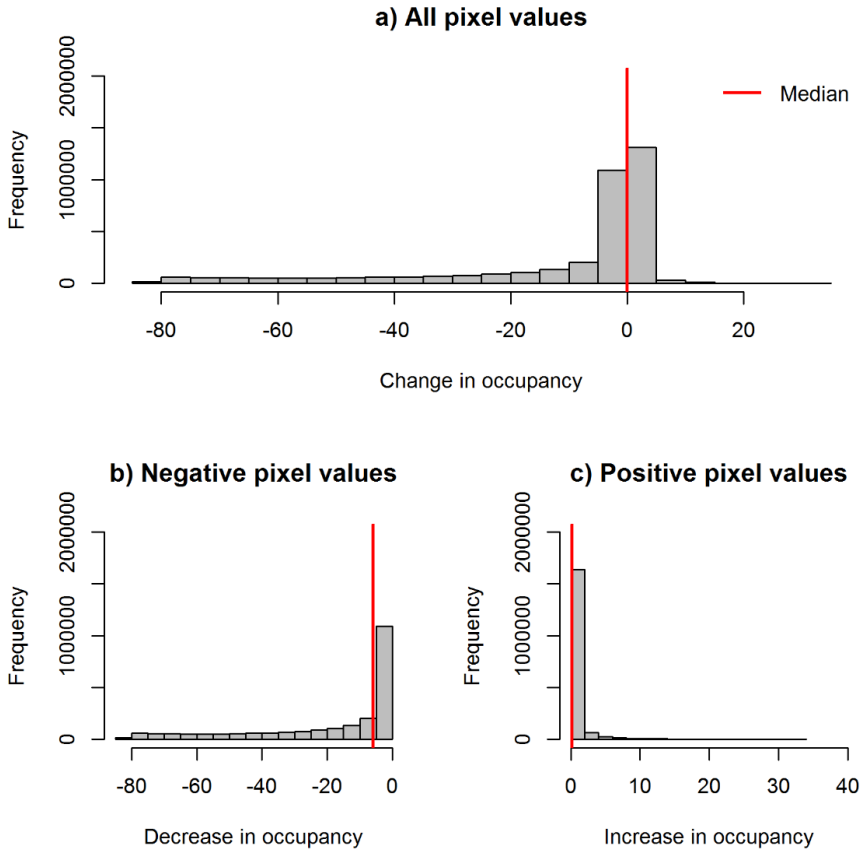


Figure SI IV-9: Distribution of occupancy decrease between 1985 and 2015 (low, medium and high decline) among land-use change classes (forest to pasture and forest to cropland).

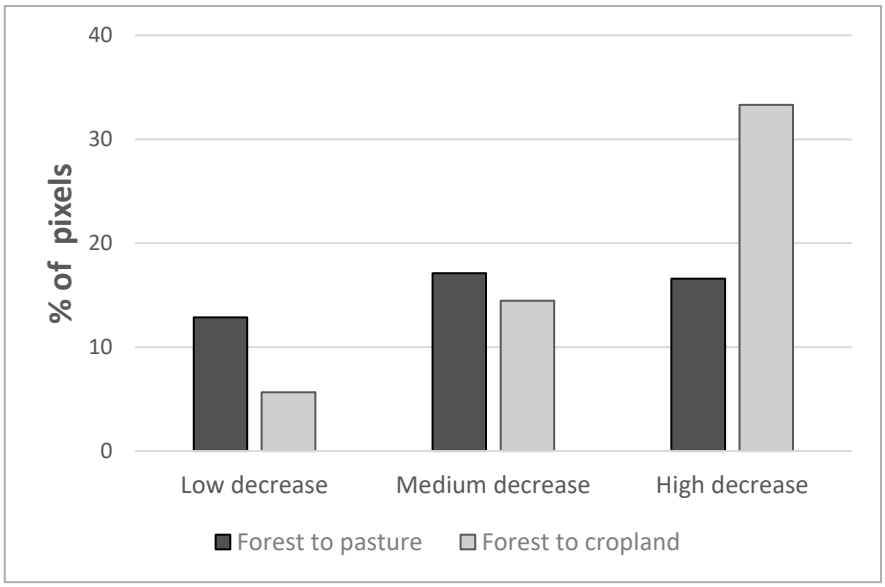


Figure SI IV-10: Share of occupancy change classes (increase/stable, low, medium and high) between 1985 and 2015 inside protected areas.

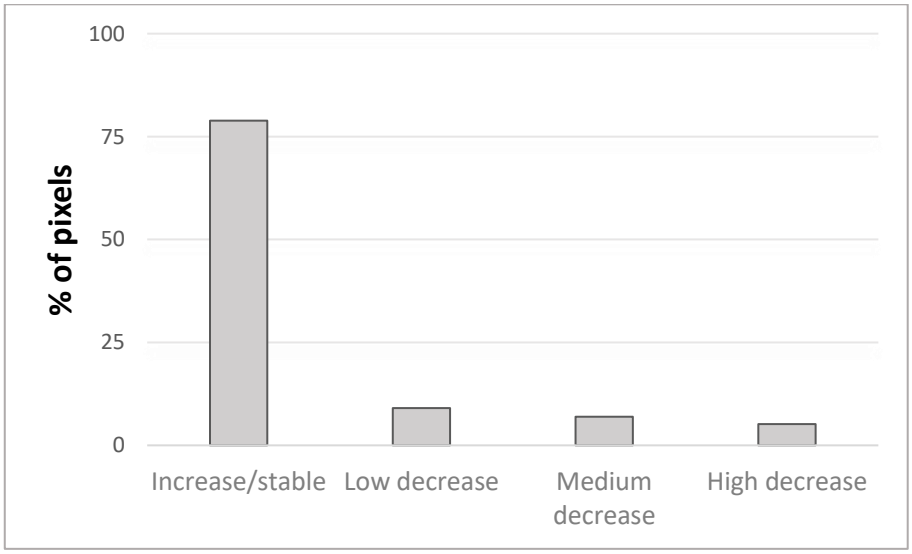
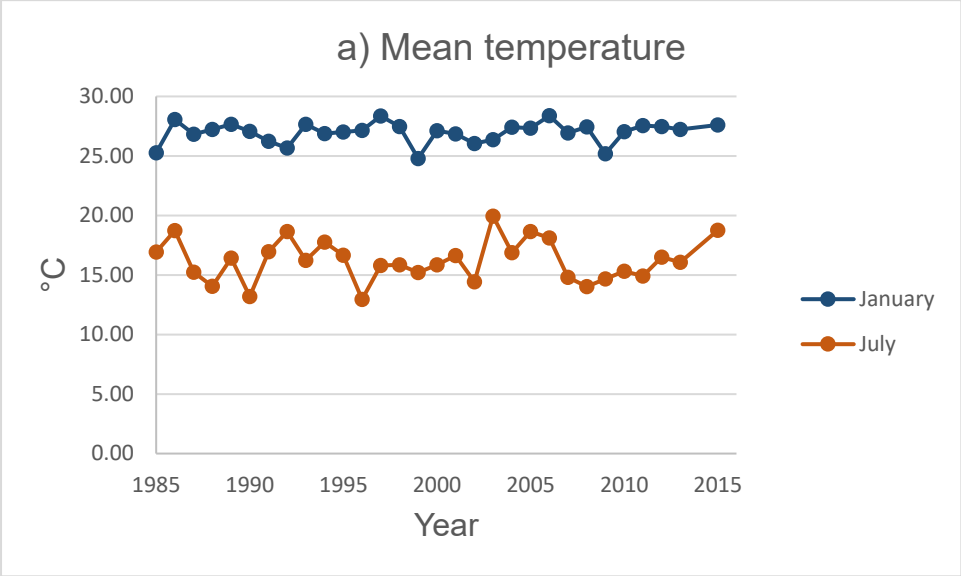


Figure SI IV-11: Variation in temperature and precipitation between 1985 and 2015. The graph includes a) mean temperature for the warmest and the coldest months (i.e., January and July respectively) and b) precipitation. Climate parameters for each year are calculated using the data from a weather station located in the Chaco Province. Data has been provided by the Argentine National Institute of Agrarian Technologies (INTA).



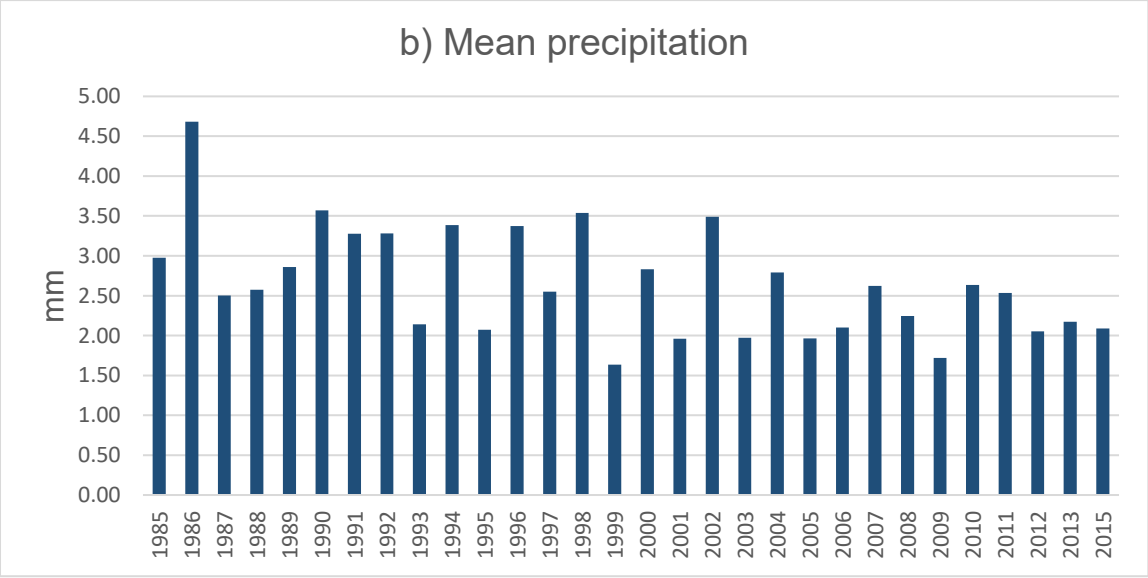
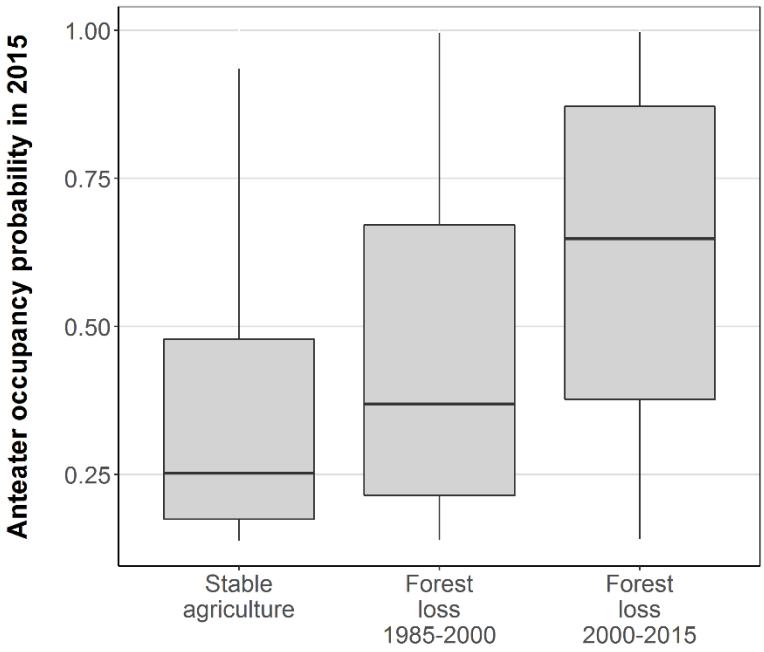


Figure SI IV-12: Distributions of predicted anteater occupancy values in 2015 for stable agriculture, areas deforested in 1985-2000, and areas deforested in 2000-2015. Stable agriculture includes pixels that were already agriculture in 1985, areas deforested in 1985-2000 pixels that changed from forest to cropland or pasture between 1985 and 2000, and areas deforested in 2000-2015 pixels that changed from forest to cropland or pasture in between 2000 and 2015.



Chapter V:

Biodiversity loss in deforestation frontiers: Linking occupancy modelling and physiological stress indicators to understand local extinctions

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Abstract

Tropical deforestation is a main driver of the global biodiversity crisis. Impact assessments typically focus on species' presence, which means impacts are detected when local extinctions have occurred – and thus when it is too late. Here, we pioneer the combined use of two approaches that can detect deforestation impacts earlier, at the level of populations (using occupancy modelling) and at the level of individuals (using stress hormonal indicators). We tested this approach for the collared peccary (*Pecari tajacu*) in the Argentine Chaco, a global deforestation hotspot. We used camera-trap data to model peccary occupancy in relation to woodland cover and loss, and measured glucocorticoid metabolites in peccary feces to assess individuals' stress level in deforestation areas. We found that peccary occupancy was highest in remote areas with high woodland cover, but low otherwise. Peccaries were typically absent from areas where deforestation had been widespread recently. Where peccaries were present, physiological stress was correlated with the extent of edge between cropland and forest (a proxy for food availability), and not with deforestation. This, and the observation that peccaries disappear quickly as deforestation progresses, suggests that peccaries do not adapt well to the new conditions in deforestation frontiers. In terms of conservation management, our results underpin the importance of protecting large, contiguous woodland blocks to prevent large mammals from going extinct in deforestation frontiers. More broadly, we show how combining stress hormonal indicators and occupancy modelling can provide deep insights into processes underlying local extinctions in dynamic landscapes.

1 Introduction

Habitat loss and fragmentation due to land-use changes are among the main causes of extinctions (Ehrlich & Pringle 2008). These threats are destined to continue, as global consumption of agricultural products will increase (Tilman *et al.* 2011), pushing agricultural expansion further into remaining natural ecosystems. This is particularly worrying for the tropics and subtropics, which harbor exceptional biodiversity, where deforestation is currently widespread, and where current and possible future extinction rates are highest (Laurance, Sayer & Cassman 2014; Kehoe *et al.* 2017). Understanding the effects of land-use changes on biodiversity in these deforestation frontiers is therefore crucial.

There has been a strong focus in biodiversity research on determining where species disappear. These local extinctions, however, are preceded by periods of population decline; local extinction is only the endpoint of a longer process (Ceballos, Ehrlich & Dirzo 2017). Consequently, indicators of species presence (e.g., occurrence models) may be suboptimal from a conservation perspective, as they detect impacts when species have already gone extinct, which is too late for proactive conservation actions (Ellis, McWhorter & Maron 2012). Additionally, occurrence models do not distinguish between areas where a species is abundant versus scarce, or areas where populations are stable versus declining. Together, this can lead to inaccurate conclusions regarding species' local extinction (Ashcroft *et al.* 2017). There is a great need for going beyond simplistic presence indicators to assess land-use impacts on biodiversity.

Abundance models have become a promising tool for monitoring abundance changes; however, their application in conservation is often constrained by unavailability of appropriate data. Collecting such data is costly, especially for species that can be identified individually only through genetic analyses (Gardner, Royle & Wegan 2009). Modelling occupancy can be a feasible alternative, as occupancy typically correlates with abundance (Linden *et al.* 2017; Parsons *et al.* 2017). In addition, occupancy models account for imperfect detection (i.e., false absences), therefore correcting for potential bias, which is crucial when working with elusive or scarce species (MacKenzie *et al.* 2002).

Going from simple occurrence estimations to assessing changes in abundance is a major step forward, but for species that respond with a time-delay to landscape transformations, population declines might take a long time to manifest (Kuussaari *et al.* 2009). Assessing how land-use change impacts species at the individual level can thus provide an earlier warning for populations at risk (Dantzer *et al.* 2014). A promising new tool for this is the use

of hormones as indicators of stress (Wikelski & Cooke 2006). After an individual faces a stressor, such as habitat transformation or hunting, it responds by increasing stress hormone levels (Sapolsky, Romero & Munck 2000). Specifically, glucocorticoids hormones help to cope with the acute stressor and individuals that are subject to chronic stress may have permanently constant glucocorticoid levels. Chronic stress can decrease reproductive success, suppress growth or immune system functions, which can reduce individual fitness (Sapolsky, Romero & Munck 2000). The concentration of glucocorticoids in body fluids, or their metabolites in excreta, can be precisely measured and thus inform about individuals' stress level (Sheriff *et al.* 2011). The measurement of fecal glucocorticoids metabolites (FGMs) is particularly useful since it provides an efficient and non-invasive procedure to assess stress in free-ranging animals (Palme 2019).

Even though glucocorticoids offer advantages to investigate the effects of land-use changes on biodiversity, many gaps in our understanding remain. The few studies that have used such indicators in this context have done so by focusing on single points in time, thus assessing the effects of habitat availability rather than the effects of land-use change. Moreover, existing studies come to diverging conclusions on the relationships between glucocorticoid levels and habitat availability or quality: Balestri *et al.* (2014) and Janin, Léna and Joly (2011) found a negative relationship, while Pokharel *et al.* (2018) and Munshi-South *et al.* (2008) found a positive relationship. Furthermore, very few studies have assessed the combined effect of various threats (e.g., habitat loss and hunting) (Wasser *et al.* 2011; Rimbach *et al.* 2013). To our knowledge, only one study has combined stress hormonal indicators with occurrence data to understand the relationship between habitat availability and fragmentation and the distribution and physiological state of common toads in south-eastern France (Janin, Léna & Joly 2011). No study has assessed land-use change impacts by linking occupancy models and stress indicators in deforestation frontiers.

Tropical and subtropical dry forests are among the most threatened ecosystems due to rapid agricultural expansion (Miles *et al.* 2006; Hansen *et al.* 2013). Yet, these systems remain under-researched (Blackie *et al.* 2014), translating into barriers for conservation planning and action. The Gran Chaco, considered the largest dry forest in the world, is a highly dynamic deforestation frontier. Since the 1990s, the region experiences among the highest deforestation rates worldwide, mainly due to the expansion of cattle ranching and soybean production (Baumann *et al.* 2017). As a consequence, the region is undergoing massive defaunation (Quiroga *et al.* 2014; Núñez-Regueiro *et al.* 2015; Periago, Chillo & Ojeda 2015; Semper-Pascual *et al.* 2018). How species of conservation concern respond to land-

use changes in the Chaco, however, is poorly understood, in part because the few existing studies used occurrence models only (Núñez-Regueiro *et al.* 2015).

The overall goal of our study was to assess how large mammals respond to land-use changes by combining occupancy models to assess pressure at the population level, and FGM measurements to assess pressure at the individual level (Figure V-1). We chose the collared peccary (*Pecari tajacu*) in the Argentine Dry Chaco as a model system. The collared peccary occurs from the southern United States to northern Argentina, where the Chaco has among the lowest densities of collared peccaries across their range (Melletti & Meijaard 2017). Main threats in the Chaco are over-hunting and habitat loss, which have resulted in the species' widespread extirpation (Oliver & Brisbin 1993). Both these pressures are high and rising (Altrichter 2005; Baumann *et al.* 2017; Camino *et al.* 2018). However, it is unknown how peccaries respond to these stressors and whether they can cope with the widespread landscape transformation the Chaco currently experiences.

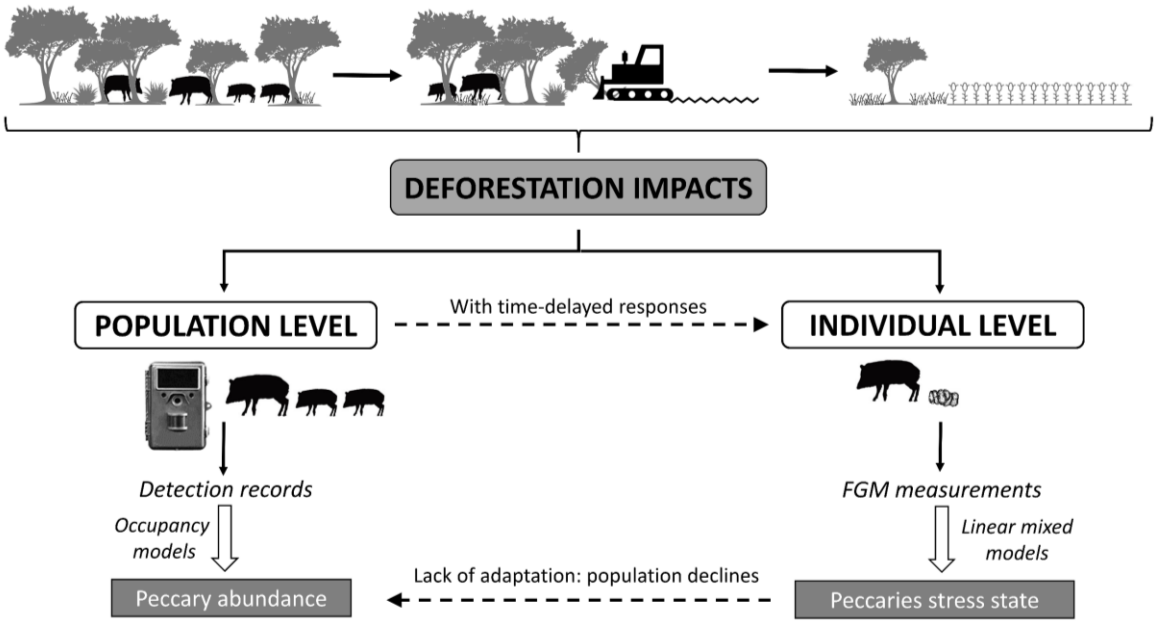

Figure V-1: General approach we used to assess the effects of deforestation on peccaries at population and individual level. At the population level, we used camera-trap data and occupancy models to estimate abundance of peccaries in relation to woodland extent and loss. At the individual level, we used stress hormone measurements (fecal glucocorticoid metabolites, FGMs) and linear mixed models to assess the stress level in relation to woodland loss and associated threats. If there are time-delayed responses, population declines may take a long time to manifest, and the deforestation impacts need to be assessed at the individual level. If individuals do not adapt to the new environmental conditions, population declines may occur.

We combined occupancy modelling and stress hormone analyses to test which variables affect peccaries at both the population and individual level. Specifically, we asked:

1. How do woodland availability and loss relate to peccary occupancy?
2. How do woodland availability and loss relate to FGM measurements, and how strong is this relationship in comparison to other human threats?

2 Material and methods

2.1 Study area

Our study area is in the Gran Chaco (Figure V-2), an ecoregion extending into Argentina, Paraguay, Bolivia and Brazil.

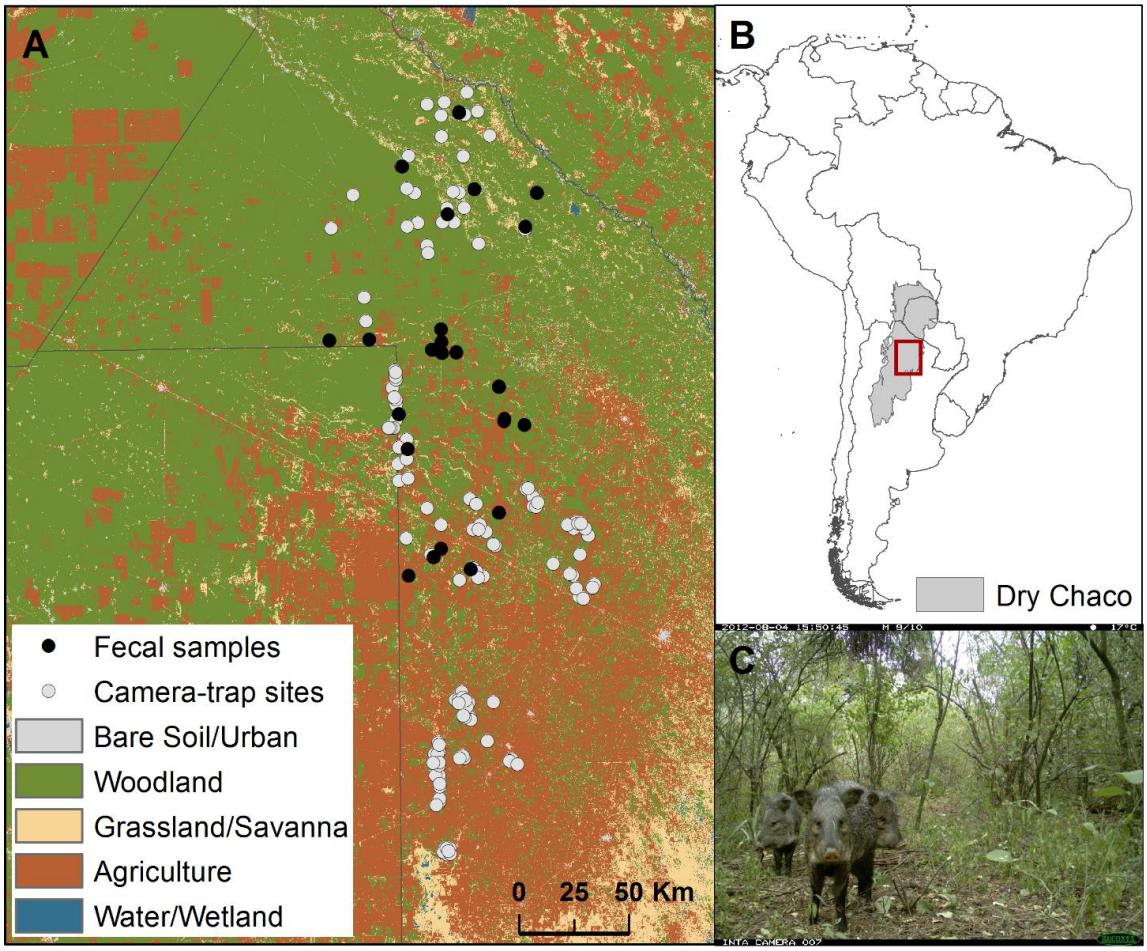

Figure V-2: Location of the study area in A) northern Argentine Dry Chaco, including camera-trap and fecal sampling sites, and B) South America. Picture C) shows collared peccary captures on a camera-trap.

The Chaco harbors high levels of biodiversity and endemism (TNC et al. 2005), as well as all three species of peccaries (collared, white-lipped and Chacoan peccary). We conducted the study in the northern Argentine Dry Chaco, an area with a highly seasonal climate.

Natural vegetation consists of woodlands with interspersed shrublands, grasslands, and savannas. Over the last decades, agriculture in the Argentine Dry Chaco has expanded rapidly (~20% of woodland converted since 1985, Baumann *et al.* (2017) Baumann et al. (2017)), and the southern part of our study area is one of the most active deforestation frontiers in the entire Chaco (Piquer-Rodríguez *et al.* 2015). However, agricultural expansion has not yet reached the northernmost part of our study area, which still contains continuous and well-preserved woodland patches (Figure V-2), including two National Parks (Copo National Park, ~118,100 ha and El Impenetrable National Park, ~137,200 ha). This north/south gradient of woodland loss provides an interesting case for studying the effects of past and recent deforestation on biodiversity.

2.2 Collared peccary data

We used camera-trap data from three surveys to model peccary occupancy: survey1 was carried out in 2013 in the center of our study area (Decarre 2015), survey2 in 2014–2015 in the southern part (Gómez-Valencia 2017), and survey3 in 2016–2017 in the northern part (Proyecto Quimilero) (Figure V-2). Cameras were deployed using a stratified random sampling design (Text SI V-1). Sites were selected with a minimum distance of at least 1 km between them. The mean distance between sites was 3.78 km (minimum distance = 1.01 km; maximum distance = 22.12 km) and thus substantially larger than the average peccary home range (Table SI V-1).

We measured FGM measurements in 66 fecal samples collected from 23 different sites in July–October 2017 (mean number of feces per site: 2.9; range: 1–6). Given that FGM measurements may be affected by bacterial or microbial degradation after defecation (Sheriff *et al.* 2011), we followed an opportunistic sampling design in order to collect enough fresh feces (i.e., same day excretion). We contacted locals (e.g., smallholders living in the forest, hunters) to gather information about potential peccary locations, and searched in areas where peccaries were recently seen. We identified fresh feces by its wetness and odor. On site, feces were placed in plastic bags and immediately ice-stored. Later the same day, samples were frozen (−20 °C) until further processing.

2.3 FGM analysis

In the laboratory, we extracted FGMs by adding 5 mL methanol/ water (80%) to a portion (0.5 g) of each well-homogenized sample (Palme *et al.* 2013). After shaking (2 min) and centrifugation (15 min, 3000 G), we separated an aliquot (0.5 mL) from the supernatant for

further use. We evaporated the extracts at 60 °C, resuspended in 80% methanol and dissolved (1:4) in an enzyme immunoassay buffer. We used a previously validated immunoassay for the species (Coradello *et al.* 2012), employing a cortisol-R4866 antibody (supplier Coralie Munro, University of Davis, California). We ran all measurements twice and used the mean value. The intra-assay coefficients of variation (CV) were 20%, 50% and 80% for controls containing low, medium and high concentrations of cortisol standard, respectively. The inter-assay CV for the standard of kit was 2.5%.

2.4. Modelling collared peccary occupancy

We estimated peccary occupancy as a proxy for pressure from land-use change at the population level. We used a likelihood-based, single-season occupancy model (MacKenzie *et al.* 2002) to estimate peccary occupancy (Ψ) in relation to landscape and human pressure variables, while accounting for detectability (p). This framework uses data from sampling sites that were visited multiple occasions to estimate detection probability. Even though we deployed the camera-traps during three different seasons (2013, 2014–2015 and 2016–2017), each site was visited during one single season to ensure that sites were closed to changes in occupancy. We were unable to formally check for spatial autocorrelation, as the response variable of interest (i.e., occupancy) was only partially observed (Burton *et al.* 2012; MacKenzie *et al.* 2017). Nevertheless, spatial autocorrelation should not be a problem, as the independence assumption of occupancy models relates to the observation process (i.e., detection) rather than to the occupancy, and spatial autocorrelation can be accounted for with an appropriate sampling design (MacKenzie *et al.* 2017). We sought to minimize potential autocorrelation issues by selecting sites randomly and within a minimum distance (see Section 2.2). To generate sampling occasions, we pooled daily detection/non-detection records for each camera-trap site into consecutive camera-days. We carried out sensitivity analyses to understand how the length of each sampling occasion affected detection and occupancy estimates, and defined a sampling occasion as a seven-day interval (Figure SI V-1). To ensure a minimum of three sampling occasions per site, we discarded sites with < 21 camera-days. Additionally, we only used a maximum of 12 sampling occasions per site to ensure the closure assumption of occupancy models was met. The final dataset consisted of 137 sites, with a mean of 6 sampling occasions (range 3–12) and a mean sampling effort of 42.2 camera-days (21–84) per site.

To model peccary occupancy, we followed a two-step approach using the R package *unmarked* (Fiske & Chandler 2011). First, we modelled detection probability by including

only predictors that may affect detection. Detection predictors included variables related to the sampling protocol, as well as variables that may affect peccary activity, and thus detectability. In total, we tested five predictors: *survey*, *effort*, *temperature*, *precipitation* and *distance to roads* (Table SI V-2). We checked for collinearity between predictors (Pearson's $r \geq 0.7$), and given the absence of correlation, we considered all possible predictor combinations. We also considered the quadratic form of *temperature*, as we hypothesized that peccaries detection may be less likely during extreme (low and high) temperatures. We used Akaike's Information Criterion, corrected for small sample size (AICc; Burnham and Anderson (2002)), ranked models using ΔAICc, and selected the one with the lowest ΔAICc as the best detection probability model.

Second, we modelled occupancy probability while keeping the best- fitting detection model constant and included predictors that affect occupancy. Given that the main threats to peccaries in the Chaco are habitat loss and over-hunting (Oliver & Brisbin 1993), we selected predictors representing (1) habitat availability and loss, and (2) hunting pressure (Table SI V-2). As habitat-related predictors, we included *woodland cover*, *past woodland loss* (between 1985 and 2000), *recent woodland loss* (2000–2015) and *total woodland loss* (1985–2015). We used a high-resolution (30 m) land-cover map from 2013 (Baumann *et al.* 2017) for the camera-trap data collected in 2013, and an updated land-cover map from 2015, consistent with Baumann et al., 2017 (Figure SI V-2) for the camera-trap data collected between 2014 and 2017. To calculate *woodland loss*, we used land-cover maps from 1985, 2000 and 2015, again consistent with Baumann et al. (2017) (Figure SI V-2). We derived habitat predictors in a circular buffer around each camera-trap site. We tested different buffer sizes: 500 m, 1000 m and 1500 m radius, with 1000 m representing the radius of an average, circular peccary home range (Table SI V-1). The hunting-related predictors were *distance to homesteads*, *distance to settlements* and *distance to roads* (Table SI V-2). Among correlated predictors for occupancy modelling (Pearson's $r \geq 0.7$), we retained the one with the lowest AICc in a univariate model (Table SI V-2).

We built a first set of candidate models testing all possible combinations of habitat-related predictors. Next, we built a second set of models testing all possible combinations of hunting-related predictors. Finally, we built a third set of candidate models by adding all the hunting-related predictors to the models from the first set (i.e., only habitat-related variables). This allowed us to assess whether occupancy was driven by human-related variables, hunting-related variables, or the combination of both. We compared all candidate models (i.e., models including and excluding hunting-related predictors) using AICc and

considered models with a ΔAICc < 2 to be equally well-supported. We model-averaged coefficients across the top models (ΔAICc < 2) and tested goodness-of-fit on the global model using 10,000 bootstrap replicates and the Pearson $\chi 2$ statistics (MacKenzie & Bailey 2004).

2.4 Modelling FGM measurements

To test whether land-use changes influence hormonal stress in collared peccaries, we used linear mixed models. Peccaries occur in herds of typically 5–25 individuals (Taber *et al.* 1994; Judas & Henry 1999). To account for feces collected at a given site likely coming from individuals belonging to the same herd, we used *site* as a random factor in our models. We log-transformed the response variable (i.e., FGM measurements) to meet the normality assumption. We hypothesized that FGM measurements were possibly influenced by land-use change, hunting pressure and food availability. Thus, we selected three predictors representing land-use changes; two related to habitat availability/loss (*woodland cover*, *division index* and *deforestation index*) and one related to agricultural expansion (*extent of cropland*); three predictors representing hunting pressure (*distance to settlements*, *distance to homesteads* and *density of roads*), and one predictor representing food availability from cropland (extent of *edge* between woodland and cropland) (Table SI V-3). Although we were unable to measure food availability directly, we found many signs of peccaries feeding in croplands near woodland patches, such as half-eaten corn cobs or pumpkins, as well as tracks between woodland patches and nearby cropland. Also, locals reported peccaries frequently feeding in croplands close to woodlands. We thus used the extent of edge between forest and cropland as a proxy for food availability to peccaries. When two predictors belonging to the same category were correlated (Pearson's $r \geq 0.7$), we retained the one with the lowest AICc in a univariate model (Table SI V-3). To derive the land-use predictors, we updated the 2015 land-cover map described above using the monthly deforestation reports from GUYRA Paraguay (http://guyra.org.py/informe-deforestacion) together with Landsat images from 2017. We tested the same buffer sizes (500 m, 1000 m and 1500 m).

To determine which factors influence FGM measurements, we performed model selection across models representing different hypothesis: the habitat hypothesis ($H_{habitat}$: stress levels, as measured by FGMs, are influenced by habitat availability and loss), the hunting hypothesis ($H_{hunting}$: stress levels are influenced by hunting pressure), the food availability hypothesis (H_{food}: stress levels are influenced by food available from croplands next to woodland patches) and the cropland expansion hypothesis ($H_{crop\text{-}ext}$: stress levels are

influenced by cropland extent). We also considered combined hypothesis (e.g., both habitat and hunting affect FGMs), but only in models including non-correlated predictors (Pearson's $r \geq 0.7$) (Table SI V-4). We used AICc to select the best model and we considered as competing models those with $\Delta AICc < 2$.

3 Results

3.1 Population level: collared peccary occupancy

From 5782 camera-days, we obtained 46 independent peccary captures (mean capture rate = 0.80 captures/100 camera-days). Across all sites, the estimated detection probability was 0.26 (SE = 0.04), and the occupancy probability was 0.16 (SE = 0.04). Our best-fitting detection model included *distance to roads* and *effort*, indicating that detection improved when cameras were deployed closer to roads and for a longer time period. Additionally, the best-fitting model contained the predictor *survey*, suggesting that detection probability varied among the three surveys.

Occupancy probability was best explained at the 500 m spatial scale, with all best models (i.e., $\Delta AICc < 2$) including mainly habitat-related predictors (Table V-1). *Woodland cover* was the most important predictor, followed by *distance to roads*, *recent woodland loss* and *past woodland loss* (Table V-1). Model-averaged coefficients also corroborated that *woodland cover* was the most important predictor, and that peccary occupancy was higher in sites with high woodland cover (Table V-2 and Figure V-3). *Woodland loss* had a negative effect on peccary occupancy, and the effect of recent (after 2000) woodland loss was higher than the effect of past woodland loss (i.e., before 2000; Table V-2). *Distance to roads* was positively correlated with peccary occupancy (Table V-2). The goodness-of-fit test for the global model indicated that our model fitted the data adequately and that there was no over-dispersion ($p = 0.10$; $\hat{c} = 1.57$).

Table V-1: Candidate models for peccary occupancy (both detection and occupancy probability) and FGM ranked according to Akaike's Information Criterion corrected for small sample size (AICc). For the occupancy models (both detection and occupancy probability), only best models and the null model are presented. For the detection models, best-fitting model is shown in bold. For the occupancy and FGM models, models with ΔAICc<2 are shown in bold. ΔAICc indicates the difference between the AICc of a model and the model with the lowest AICc value. $AICc_w$ represents Akaike's Information Criterion weight.

Model	Variables	AICc	ΔAICc	$AICc_w$
Occupancy models				
Detection				
DM_12	**p (Roads + Effort + Survey) ~ Ψ (1)**	**228.09**	**0.00**	**0.27**
DM_28	p (Roads + Effort + Survey + Temp) ~ Ψ (1)	229.06	0.97	0.17
DM_16	p (Roads + Effort + Prec + Survey) ~ Ψ (1)	229.40	1.30	0.14
DM_null	p (1) ~ Ψ (1)	253.97	25.88	0.00
Occupancy				
OM_1	**p (Roads + Effort + Survey) ~ Ψ (Wood)**	**225.18**	**0.00**	**0.18**
OM_16	**p (Roads + Effort + Survey) ~ Ψ (Roads)**	**225.65**	**0.47**	**0.32**
OM_6	**p (Roads + Effort + Survey) ~ Ψ (Wood + WoodLoss_recent)**	**226.32**	**1.14**	**0.42**
OM_7	**p (Roads + Effort + Survey) ~ Ψ (WoodLoss_past + WoodLoss_recent)**	**227.08**	**1.89**	**0.49**
OM_Null	p (Roads + Effort + Survey) ~ Ψ (1)	253.97	28.79	1.00
FGM models				
M_food	**FGM ~ Edge**	**142.03**	**0.00**	**0.52**
M_hab_food	FGM ~ Div + Defo + Edge	144.85	2.82	0.13
M_null	FGM ~ 1	144.98	2.95	0.12
M_hab	FGM ~ Div + Defo	145.64	3.60	0.09
M_crop	FGM ~ Crop	145.93	3.90	0.07
M_hunt_food	FGM ~ Sett + Home + DensRoads + Edge	147.09	5.06	0.04
M_hab_crop	FGM ~ Div + Defo + Crop	147.92	5.88	0.03
M_hunt_crop	FGM ~ Sett + Home + DensRoads + Crop	150.96	8.93	0.01
M_hunting	FGM ~ Sett + Home + DensRoads	151.25	9.22	0.01
M_hab_hunt	FGM ~ Div + Defo + Sett + Home + DensRoads	152.07	10.04	0.00

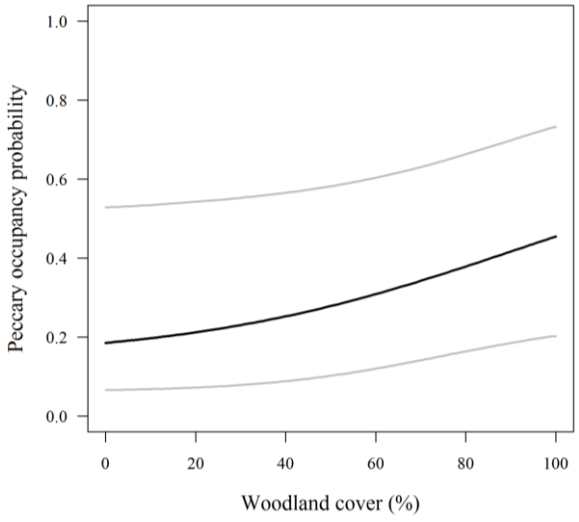

Figure V-3: Peccary occupancy probability in relation to woodland cover (we used the model-averaged coefficients across the top models, i.e., ΔAICc < 2). Light gray lines represent the 95% confidence interval.

Table V-2: Coefficient estimates (β) and 95% confidence intervals (95% CI) for the top four occupancy models and the model average. All variables are standardized to 0 mean and 1 standard deviation for comparison.

	OM_1		**OM_16**		**OM_6**		**OM_7**		**Avg.**	
Detection	β	95% CI	β	95% CI	β	95% CI	β	95% CI	β	95% CI
Intercept	-6.07	-8.57, -3.58	-5.77	-8.38, -3.16	-6.01	-8.52, -3.49	-6.07	-8.57, -3.57	-5.97	-8.52, -3.43
Roads	-0.39	-0.64, -0.14	-0.44	-0.68, -0.20	-0.39	-0.64, -0.15	-0.39	-0.64, -0.15	-0.40	-0.65, -0.16
Effort	0.89	0.25 , 1.54	0.90	0.27, 1.53	0.91	0.26, 1.55	0.91	0.26, 1.57	0.90	0.26, 1.54
Survey1	4.48	1.58, 7.38	3.97	1.16, 6.79	4.65	1.70, 7.60	4.84	1.89, 7.79	4.42	1.46, 7.38
Survey3	4.32	2.04, 6.62	4.09	1.61, 6.57	4.25	1.93, 6.56	4.31	2.02, 6.60	4.24	1.88, 6.60
Occupancy										
Intercept	-0.79	-2.00, 0.42	-0.46	-1.50, 0.57	-1.12	-2.57, 0.32	-1.14	-2.54, 0.26	-0.81	-2.16, 0.53
Wood	1.00	0.09, 1.91			0.79	-0.11, 1.69			0.53	0.00, 1.85
Roads			0.83	-0.10, 1.76					0.24	-0.10, 1.76
WoodLoss past							-0.67	-1.58, 0.24	-0.09	-1.58, 0.24
WoodLoss recent					-0.86	-2.71, 0.99	-1.39	-3.11, 0.33	-0.37	-2.94, 0.80

3.2 Individual level: FGM measurements

FGM measurements ranged between 21.09 and 477.94 (ng/g) (mean = 124.40 ng/g). Models including predictors summarized for 1000 m buffers performed best. There was only one best-fitting model, as no other model performed equally well (ΔAICc < 2). FGM measurements were best explained by edge (Table V-1), indicating that peccaries' stress level is best explained by food availability (note that our measure of food availability is only indirect). Log-transformed FGMs decreased as the proportion of woodland-cropland edge increases (estimate ± SE = −0.29 ± 0.12). Goodness-of-fit measures for that model indicated that variance in our data was mainly explained by the random factor (i.e., site) rather than the fixed factor (i.e., *edge*; $R^2_m = 0.13$; $R^2_c = 0.52$).

4 Discussion

Tropical deforestation is a major threat to global biodiversity, and understanding how deforestation impacts species before they disappear is important for timely conservation action. Using collared peccaries in the Argentine Dry Chaco as an example, we combined two approaches that can provide insights into possible impacts of threats associated with land-use changes on (1) species' populations (i.e., occupancy estimates) and (2) individuals (i.e., FGM measurements). At the population level, we found that peccary occupancy was higher where more woodland remains and that peccaries disappear quickly as deforestation progresses. This can be explained by the combined impact of decrease peccary habitat availability and the often strong increase in hunting pressure in fragmented landscapes and along roads. At the individual level, our proxy for food limitation was the main factor correlating with physiological stress levels in peccaries, whereas woodland loss was not influencing stress levels significantly. Together, these results suggest that peccaries are highly vulnerable to a range of pressures in deforestation frontiers, including hunting. Two main insights for large mammal conservation in deforestation frontiers arise from our work. First, large mammals may not show substantial time-delayed responses to deforestation, as collared peccaries in our case. Reactive and swift conservation actions are therefore required to prevent their extirpations. Second, our work supports the view that large, contiguous woodland patches are needed to maintain large mammals in regions undergoing deforestation. More broadly, our study shows how combining FGM measurements and occupancy models can broaden understanding of processes underlying local extinctions.

Overall, peccary occupancy was best explained by habitat-related variables. Among the predictors we tested, woodland cover was most strongly correlated with peccary occupancy, with highest occupancy probabilities for high woodland cover. This is in line with prior work and can be explained by the provisioning of resources and refuges that larger woodlands provide (Altrichter & Boaglio 2004; Periago *et al.* 2017). Yet, our study is, to our knowledge, the first to investigate the effect of past and recent deforestation on peccaries. Peccary occupancy was negatively affected by woodland loss, and interestingly, recent deforestation, had a higher effect than past deforestation, suggesting that peccaries respond quickly to habitat loss, similar to other large mammals in the tropics (Rocha *et al.* 2018).

Although our results suggest that habitat loss was the most important driver of peccary decline in the Argentine Chaco, hunting pressure may also play an important role. Generally, the collared peccary is one of the most hunted species in the Chaco (Altrichter 2005; Camino *et al.* 2018). Peccaries avoided areas close to roads, likely because of the high hunting pressure that exist along roads, as roads facilitate access by hunters to woodland patches (Altrichter & Boaglio 2004; Benítez-López *et al.* 2017). There are likely also large synergistic effects between habitat loss and hunting (Corlett 2007). The Chaco woodlands are characterized by dense and thorny vegetation (Huntley 1982) and moving through these woodlands can be extremely challenging. Consequently, land-use changes themselves make many areas accessible to hunters, who access woodland patches that would otherwise be inaccessible, or kill individuals when they move between woodland patches (Altrichter 2005). In other words, we hypothesize that although hunting might lead to the ultimate extirpation of peccaries from a landscape, it can do so only because deforestation fragments landscapes.

FGM measurements were not significantly correlated to woodland extent or woodland loss, contrary to the prediction of our habitat hypothesis ($H_{habitat}$). One reason was likely that we did rarely find feces in areas where woodland loss was high and woodland extent low (Figure SI V-3), since peccaries rarely survived in such areas long enough. Likewise, we did not find a direct association between FGM measurements and our variables proxying hunting pressure ($H_{hunting}$). Previous studies suggested that individuals from fragmented or degraded landscapes are more stressed than individuals from well-preserved landscapes (Janin, Léna & Joly 2011; Balestri *et al.* 2014). Likewise, caribou living in areas with high human activity had higher FGM concentrations than caribou from areas with low human activity (Wasser *et al.* 2011). To our knowledge, only one study has used FGM measurements to assess the relationship between landscape transformation and species' stress state in tropical dry forests and savannas,

highlighting that FGM measurements in maned wolves increased with distance from natural areas in the Cerrado (Vynne, Booth & Wasser 2014). Yet, other studies found individuals from anthropogenic landscapes to have low stress levels, which was attributed to the benefits that animals may find in such landscapes (e.g., food availability or protection against poachers) (Wasser *et al.* 2004; Munshi-South *et al.* 2008).

A key finding from our analyses was that the extent of woodland-cropland interface was strongly correlated with stress levels, thus supporting our food availability hypothesis (H_{food}). This is in line with other studies. For instance, crop-raiding elephants in India had lower FGM measurements than non-raiding elephants, due to the benefits obtained from foraging in agricultural fields (Pokharel *et al.* 2018). During our fieldwork, we found clear and multiple evidence of peccaries feeding on cropland next to woodland edges (e.g., tracks, half-eaten corn cobs, reports by locals). This suggests that the extent of woodland-cropland interface could indeed represent food availability. Still, we caution that our measure of food availability was far from perfect. For example, we could neither directly measure food availability in croplands, nor in woodlands (i.e., roots, leaves or fruits). Including such information would have been beneficial to further corroborate the food hypothesis. Moreover, we assessed the importance of nearby croplands during times when they represented food resources and were relatively safe, but the relationship between FGM measurements and woodland-cropland edge may be different during other periods (e.g., when agricultural workers are present or fields are bare). Altogether, our results suggest that collared peccaries are quickly and immediately threatened by landscape transformation. Our models showed a higher correlation between recent deforestation and peccary occupancy, than between past deforestation and peccary occupancy, suggesting that there is little extinction debt. A likely explanation is again the linkage between deforestation and hunting pressure, as landscapes become more accessible and hunting pressure is particularly high during and right after deforestation takes place, as the same people employed to clear woodlands often hunt intensively (Altrichter 2006). Additionally, woody biomass is often burned on site, killing wildlife in the process (Prada & Marinho-Filho 2004). Moreover, the lack of correlation between woodland loss and stress levels suggest that peccaries are extirpated quickly, before they can acclimatize to the new conditions.

This is, to our knowledge, the first study combining occupancy models with FGM measurements to understand local extinctions in a tropical deforestation frontier. Our results showed that this approach can provide interesting and valuable insights that neither of the methods can provide alone. Nevertheless, a number of uncertainties remain. First, we

investigated the effect of extrinsic factors (i.e., habitat loss, hunting pressure) on FGM measurements, yet our analyses were purely correlative and as with any correlation analyses, this does not necessarily imply causation. Second, intrinsic factors we could not control for such as sex or reproductive status could have affected FGM measurements (Palme 2019). For instance, Pokharel *et al.* (2018) measured higher FGM levels in female elephants than in males, or Balestri *et al.* (2014) found that FGM measurements in a lemur species were higher during mating season. Yet, such differences may be lower in collared peccaries as they give birth all year around (Gongora *et al.* 2017). Still, studies typically find that extrinsic factors dominate (Pokharel *et al.* 2018; Santos *et al.* 2018). Third, inter-specific interactions such as competition or predation could affect FGM measurements. Although all three species of peccary are possibly sympatric in the most northern part of our study area, we did not find any signs of this (no scats, tracks, etc. of the other species). Predation from pumas (although rare in our study region) could have influenced stress levels, but we had no data on puma distribution or abundance. Finally, a lack of correlation between hunting-related variables and FGM measurements does not equal a lack of a hunting effect. We could use only indirect measures (e.g., distance to roads or settlements) as proxies for hunting pressure. Although such proxies are often used (Benítez-López *et al.* 2017; Romero-Muñoz *et al.* 2019), data directly capturing hunting pressure would have improved our models.

Two main implications for large mammal conservation derive from our work. First, we demonstrate that large mammals, such as peccaries, may not show time-delayed responses to landscapes transformation. This finding differs from other studies focusing on birds and smaller mammals, for which time-delayed responses were found (Semper-Pascual *et al.* 2018). As a result, where rapid and widespread deforestation occurs such as in the Chaco, swift conservation actions are needed to prevent local extinctions. Second, our study highlights that such conservation actions should focus on maintaining and protecting large, contiguous woodland patches. For the Chaco, this can be achieved by enforcing existing legislation (e.g., the Argentine Forest Law which zones woodland areas into three classes of land-use restrictions, Seghezzo *et al.* (2011)) and increasing the number of protected areas. Similarly, promoting more sustainable hunting techniques and implementing anti-poaching strategies, especially in highly fragmented areas, may help to reduce the high synergistic effects of habitat loss and hunting, for which we found evidence.

More broadly, our study demonstrates how combining occupancy models and hormonal stress indictors can help to better understand processes underlying population declines. Particularly,

our approach may help to understand how fast species respond to landscape transformation, insights that cannot be easily made using only occurrence models (Janin, Léna & Joly 2011; Ellis, McWhorter & Maron 2012). This is crucial for conservation planning, as different conservation strategies should be implemented depending on how fast species respond. For instance, habitat restoration may help to avoid local extinction for species that show time-delayed responses. However, prompt conservation strategies, such as anti-poaching patrols or strict protected areas, may help to preserve species that respond to landscape transformation immediately. Given the high deforestation rates in many parts of the world, especially in the world's tropical and subtropical dry forests (Hansen *et al.* 2013), much is at stake. Combining occupancy models and hormonal stress indictors can help to assess threats to species in dynamic landscapes, where species and populations are facing extinctions, and where data on their population trends is often scarce.

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Supplementary Information

Text SI V-1: Camera trapping.

We used data from three independent camera-trap surveys:

1. Survey1 (Decarre 2015) was carried out between August 2013 and December 2013 in the central part of the Chaco province. In total, 59 sites were selected where camera-traps were deployed in plots located in five different types of homogeneous habitat: forest (21 camera stations), forest strips (8), natural grasslands (3), silvopastures, i.e., a type of agroforestry system that combines woodland and livestock (9) and cropland (18). Sites were randomly selected for each habitat type among a number of possible sites and a random placement strategy was used inside each plot when possible, avoiding trails and at least 300m apart from the edge of the habitat. Reconyx PC800 Hyperfire Professional Camera-traps were attached to trees or wooden sticks at an average height of 30cm.
2. Survey2 (Gómez-Valencia 2017) was carried out between December 2014 and September 2015 in the southern part of the Chaco province, where 49 sites within forests of different sizes were sampled. Sampling sites were selected following the approach described in Pasher *et al.* (2013). First, the study area was divided in a regular 1,200 ha grid, with each grid cell containing a different percent of forest cover. Second, sites were selected depending on the accessibility, and the percent of forest cover, thus representing a wide gradient of forest cover in the sample. Bushnell 8MP Trophy Cam HD Hybrid Trail camera-traps were placed at a height of 40-45cm.
3. Survey3 (Proyecto Quimilero) was carried out between June 2016 and May 2017 in the northern part of the Chaco province. In total, 29 sites were selected in forest and shrubland habitats. Sites were randomly selected in a 6,000 km^2 study area, trying to avoid trails, and separated at least 6 km apart from one another. Bushnell Strike Force HD camera-traps were placed at an average high of 25cm.

Further detail about the camera placement and images processing of the two first surveys is described in Decarre (2015) and Gómez-Valencia (2017).

Text SI V-2: Division and deforestation index.

Two of the variables we included to model FGM measurements were the division index and the deforestation index. Here, we provide further details on how these were calculated.

Division index: The division index measures the probability that two randomly chosen places are not situated in the same undissected area (Jaeger 2000).

Division equals 1 minus the sum of patch area divided by total landscape area, quantity squared, summed across all patches of the corresponding patch type (McGarigal 2014). We used the ClassStat function from the R package *SDMTools* (VanDerWal et al. 2014) to derive this index.

$$\text{Division} = \left[1 - \sum_{j=1}^{n} \left(\frac{a_{ij}}{A}\right)^2\right]$$

a_{ij} = Area of patch *ij*
A = Total landscape area

Deforestation index: The deforestation index measures the degree of deforestation in the landscape considering the time since deforestation (i.e., deforestation that occurred recently has a higher effect than deforestation that occurred a long ago).

Deforestation equals the total woodland area in in the total landscape area (a buffer in our case) minus the sum of the area of all deforested patches weighted by the time since deforestation.

$$\text{Deforestation} = W_t - \sum_{i=1}^{n} (\text{Def}_i * \text{Time Def}_i)$$

W_t = Total woodland area
n = number of deforested patches
Def_i = deforested area in patch *i*
Time Def_i = Time since deforestation in patch *i*

Table SI V-1: Reported home range sizes of collared peccary.

Home range (km^2)	**Reference**
0.50	Canevari and Vaccaro (2007)
8.00	Canevari and Vaccaro (2007)
1.50	Gongora *et al.* (2017)
0.24	Sowls (1984)
8.00	Sowls (1984)
1.23	Keuroghlian, Eaton and Longland (2004)
3.05	Keuroghlian et al. (2004)
0.64	McCoy, Vaughan and Rodrigues (1990)
1.09	McCoy, Vaughan and Rodrigues (1990)
4.60	Fragoso (1994)
5.43	Fragoso (1994)
6.85	Taber *et al.* (1994)
1.57	Judas and Henry (1999)
2.43	Judas and Henry (1999)
3.22	Average of all estimates

Table SI V-2: Predictors for modelling peccary detection and occupancy probabilitiesand associated hypothesis based on Altrichter (2005); Altrichter and Boaglio (2004); Burton *et al.* (2015) and Periago *et al.* (2017).

Predictor	Description	Hypothesis	Source
DETECTION MODELS			
Survey	Camera-trap survey	Different study designs could lead to different detection probabilities	-
Effort	Number of days that the camera-traps were active	Detection probability increases with increasing survey effort	-
Temp	Mean temperature of the month when the cameras were active	Peccaries may be less active during extreme temperatures (i.e., too hot or cold)	Argentine National Institute of Agricultural Technologies (INTA) weather stations*
Prec	Mean precipitation of the month when the cameras were active and the month before	During the dry season, peccaries walk longer distances to find water and thus, detection probability increases	
Roads	Euclidean distance to the closest road (both paved and non-paved)	Survey effort in areas close to roads is higher due to the high accessibility, and thus, detection probability increases	www.ign.gob.ar; Dirección de Vialidad Provincial (DVP) – Chaco
OCCUPANCY MODELS			
Habitat availability [a]			
Woodland	Woodland cover (%)	Peccaries prefer habitats with high vegetation cover (woodland or shrubs)	Baumann et al. (2017); This study (Figure SI V-2)
WoodLoss_past	Woodland loss (%) between 1985-2000		
WoodLoss_recent	Woodland loss (%) between 2000-2015		
WoodLoss_total [b]	Woodland loss (%) between 1985-2015		
Hunting pressure			
Sett	Euclidean distance to the closest settlement	Peccaries avoid areas close to homesteads (smallholder ranchers), settlements and roads where hunting pressure is higher	www.indec.gob.ar
Home	Euclidean distance to the closest homestead		Digitization in google earth
Roads	Euclidean distance to the closest road (both paved and non-paved)		www.ign.gob.ar; Dirección de Vialidad Provincial) DVP-Chaco

* INTA weather stations consist of point data. We interpolated the point data to obtain continuous maps for our study area using Kriging

[a] Measured within a 500m, 1000m and 1500m radius from the cell containing the camera trap location.

[b] Correlated predictor ($r \geq 0.7$) removed from the final dataset for modelling occupancy.

Table SI V-3: Predictors for modelling FGM measurements in peccariesand associated hypotheses based on Altrichter and Boaglio (2004); Altrichter (2015); Ellis, McWhorter and Maron (2012), and Periago *et al.* (2017).

Predictor	Description	Hypothesis	Source
*Land-use change**			
Wood[a]	Percentage of woodland cover	Woodland provides refuge from predators and hunters, thus, decreasing adrenocortical activity	This study (Figure SI V-2); GUYRA Paraguay deforestation reports; Landsat images
Div	Landscape division index: the probability that two randomly chosen places are not situated in the same undissected area (Text SI V:2)	Peccaries living in fragmented areas increase adrenocortical activity since they are forced to cross open areas, being therefore exposed to predators or hunting	
Defo	Deforestation index: the degree of deforestation in the landscape considering the time since deforestation (Text SI V:2)	Peccaries from areas where woodland loss occurred recently show higher adrenocortical activity than peccaries from areas where woodland loss occurred long ago	
Crop	Percentage of cropland	Peccaries affected by woodland conversion to cropland increase adrenocortical activity	
Hunting pressure			
Sett	Euclidean distance to the closest settlement	Nearby settlements represent higher hunting pressure (thus high adrenocortical activity) as people often practice illegal hunting	www.indec.gob.ar
Home	Euclidean distance to the closest homestead	Nearby homesteads (smallholder ranchers) represent higher hunting pressure (thus high adrenocortical activity)	Digitization in google earth
DensRoads*	Density of roads	Roads provide access to hunters, thus, increasing adrenocortical activity	www.ign.gob.ar; Dirección de Vialidad Provincial (DVP) – Chaco
*Food availability**			
Edge	Percentage of all pixels within the buffer classified as edge between woodland and cropland	Peccaries affected by woodland loss increase adrenocortical activity, but if they have cropland next to a woodland patch they may benefit from food availability (e.g., corn), thus decreasing adrenocortical activity	This study (Figure SI V-2); GUYRA Paraguay deforestation reports; Landsat images

* Measured within a 500m, 1000m and 1500m radius from the cell containing the camera trap location.
[a] Correlated predictor (r ≥0.7) removed from the final dataset for modelling occupancy.

Table SI V-4: Candidate models and hypotheses for explaining FGM measurements. See Table SI V-3 for a detailed explanation of the reasons for including each predictor.

Model	Variables	Hypothesis
M_hab	FGM ~ Div + Defo	FGM measurements are influenced by habitat availability and loss
M_hunt	FGM ~ Sett + Homest + DensRoads	FGM measurements are influenced by hunting pressure
M_food	FGM ~ Edge	FGM measurements are influenced by food available in croplands, measured as the percentage of woodland/cropland edge
M_agri	FGM ~ Crop	FGM measurements are influenced by agricultural activities
M_hab_hunt	FGM ~ Div + Defo + Sett + Homest + DensRoads	FGM measurements are influenced by habitat availability and loss and hunting pressure
M_hab_food	FGM ~ Div + Defo + Edge	FGM measurements are influenced by habitat availability and loss, and food available in croplands
M_hab_crop	FGM ~ Div + Defo + Crop	FGM measurements are influenced by habitat availability and loss, and agricultural activities
M_hunt_food	FGM ~ Sett + Homest + DensRoads + Edge	FGM measurements are influenced by hunting pressure, and food available in croplands
M_hunt_crop	FGM ~ Sett + Homest + DensRoads + Crop	FGM measurements are influenced by hunting pressure, and agricultural activities
M_food_crop	Correlation between variables (no tested)	FGM measurements are influenced by food available in croplands, and agricultural activities
M_null	FGM ~ 1	

Figure SI V-1: Occupancy and detection probability for different sampling intervals. Occupancy and detection probability estimates (with 95% confidence intervals) for the null model and for different sampling intervals (from 4 to 10-day occasions). Both occupancy and detection estimates typically increase with the number of days per occasion. 7-day occasions were used to strike a balance between high detection estimates and small confidence intervals.

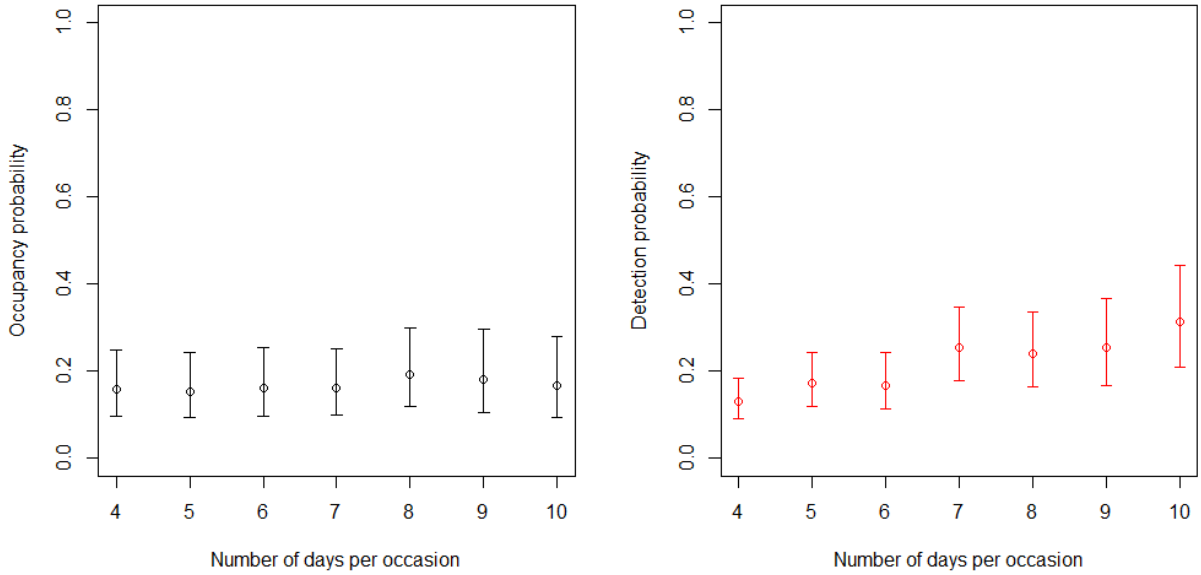


Figure SI V-2: Land-cover maps for the study region for the years 1985, 2000 and 2015. The maps for the entire Gran Chaco were derived from a total of 15,624 Landsat images using random forest classification and a large sample of training and validation data. The maps have a resolution of 30 meters. Details on the methodology are documented in Baumann et al. (2017). To account for changes in the landscape during the sampling period, we related camera-trap data to habitat-related predictors from the time period when the cameras were deployed. We related camera-trap data from 2013 (i.e., survey1) to the habitat-related predictors from the 2013 land-cover map published in Baumann et al. (2017), and we related camera-tap data collected between 2014 and 2017 (i.e., survey2 and survey3) to habitat-related predictors from the 2015 land-cover map.

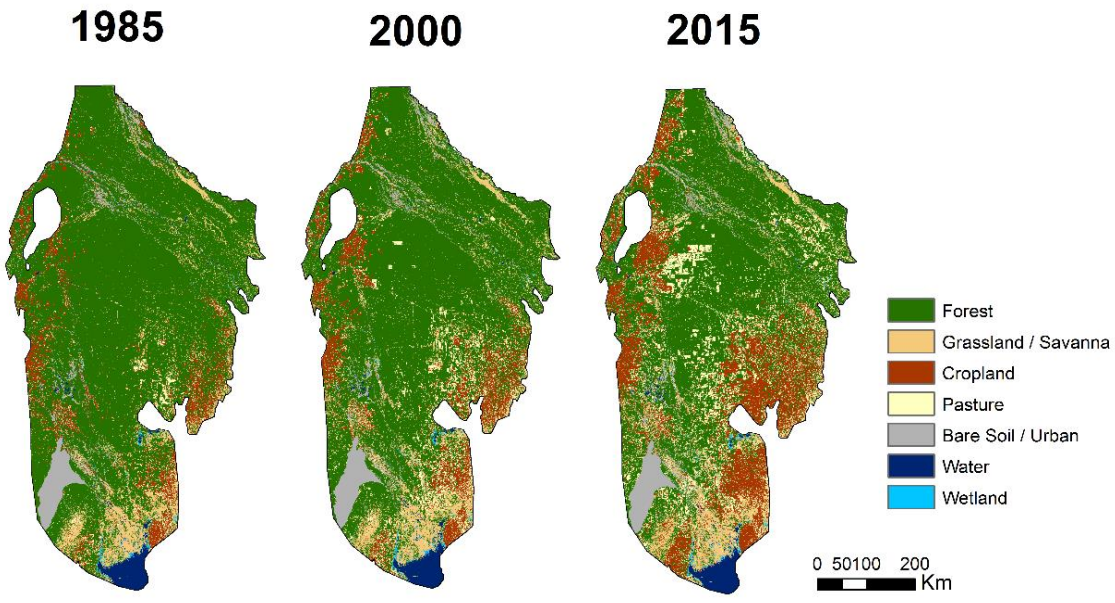
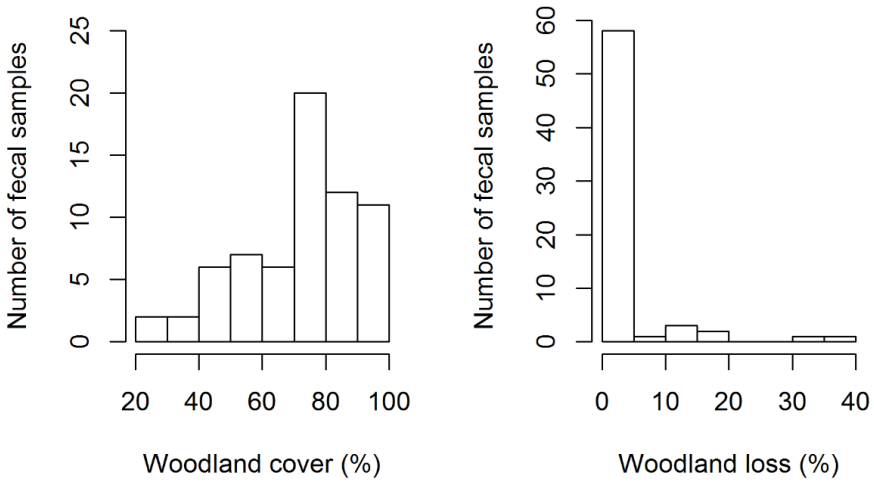


Figure SI V-3: Distribution of woodland cover and woodland loss for the fecal samples. Percentage was calculated in a 1000m radius around each sampling site. For the woodland loss histogram, we considered the total area deforested during the 12 months before the fecal sample was collected.



Chapter VI:
Synthesis

1 Summary and main conclusions

Species and populations are disappearing at an alarming rate (Ceballos *et al.* 2015; Ceballos, Ehrlich & Dirzo 2017), largely due to deforestation driven by agricultural expansion (Maxwell *et al.* 2016; Tilman *et al.* 2017; Mazor *et al.* 2018). Understanding how deforestation affects biodiversity is therefore crucial. The growing evidence of time-delayed responses of biodiversity to land-use change suggests that species are still largely influenced by past land use characteristics, and that they can persist in transformed landscapes for several years before they go extinct locally (Kuussaari *et al.* 2009; Figueiredo *et al.* 2019; Lira, de Souza Leite & Metzger 2019). Yet, studies often focus on contemporary landscape patterns when assessing the effects of land-use change on biodiversity, thus missing a window of time to avert future extinctions. This thesis helped to bridge these gaps by addressing two overarching goals. My first goal was to provide a better understanding of the individual and relative effects of past and contemporary land use on biodiversity in the Argentine Dry Chaco. My second goal was to develop approaches that capture the impacts of land-use change on biodiversity before local extinctions occur. To achieve these goals, I assessed the impacts of land-use change at multiple levels of organization (community, population and individual level) by combining extensive biodiversity datasets, land-cover data expanding over multiple years, and novel statistical approaches.

Every chapter made specific contributions to both overarching goals (Table VI-1). At the community level, I identified time-delayed responses to landscape transformation and its corresponding extinction debt. By developing a novel spatially explicit approach, I predicted the number of species predicted to go extinct due to past land-use change (i.e., extinction debt) across the entire study area. In addition, I made significant advances in the identification of which land-use change process, i.e., habitat loss or habitat fragmentation, caused the time-delayed response. At the population level, I estimated occupancy changes over time due to land-use change to highlight areas where population extinctions are more likely to occur. This approach enabled distinguishing between the direct and indirect effects of land-use change on species' populations. Finally, I used indices of physiological stress to evaluate the effects of deforestation at the individual level. I combined such indices with occupancy models to simultaneously assess the effects of deforestation at the individual and population level, thus providing a more thorough understanding of the processes underlying local extinctions.

Table VI-1: Summary of the contribution of each core chapter towards addressing each overarching goal.

		Overarching goal I: *Understand the individual and relative effects of past and contemporary land use on biodiversity in the Argentine Dry Chaco*	**Overarching goal II:** *Develop approaches that capture the impacts of land-use change on biodiversity before local extinctions occur*
Communities	**Research question I:** *Is there evidence of an extinction debt for bird and mammal communities?*	Birds and mammals showed time-delayed responses to land-use change, suggesting an extinction debt	New methods for mapping extinction debt
	Research question II: *What are the time-delayed effects of habitat loss vs. habitat fragmentation on biodiversity?*	Time-delayed responses of birds and mammals were driven by habitat fragmentation, rather than by habitat loss	Quantification of the relaxation time after habitat loss and habitat fragmentation
Populations	**Research question III:** *What are the direct vs. indirect effects of land-use change on species' populations?*	Giant anteater occupancy decreased substantially due to direct and indirect effects of land-use change	Providing spatial proxies of population change by using an occupancy framework
Populations & Individuals	**Research question IV:** *How does past and recent deforestation affect species at the population and individual level?*	Collared peccaries disappeared quickly in deforestation frontiers, due to habitat loss and hunting	Linking occupancy models and physiological stress indicators to assess deforestation impacts at the population and individual level

I used the insights gained from this research to answer the four core research questions of this thesis.

Research Question I: Is there evidence of an extinction debt for bird and mammal communities?

In Chapter II, I explored this question by investigating the relationship between contemporary species richness of birds and mammals and both contemporary and past landscape patterns. Past landscape patterns from the year 2000 explained contemporary species richness better than contemporary and 1985 landscape patterns. This indicated time-delayed responses to land-use change of 10 to 25 years, and evidence of an extinction debt for both bird and mammal communities. This evidence was particularly strong for forest specialists. The approach I developed in this chapter further allowed quantifying and mapping communities' extinction debt across the entire study area. Extinction debt maps showed that areas recently converted to agriculture had the highest probabilities of experiencing future local extinctions. In those areas, up to 56% and 29% of the extant birds and mammals, respectively, were predicted to go extinct. On the contrary, few local extinctions were predicted in areas in which large forest patches remained. The findings of this chapter have great implications for conservation practice and planning, as they indicate a window of opportunity for averting local extinctions.

Research Question II: What are the time-delayed effects of habitat loss vs. habitat fragmentation on biodiversity?

In Chapter III, I compared differences in time-delayed responses between habitat loss and habitat fragmentation by investigating the influence of annual landscape metrics on contemporary multi-species occupancy. Past extent of forest did not influence contemporary bird and mammal occupancy, indicating that both taxa responded to habitat loss immediately. However, I found that contemporary occupancy was influenced by past fragmentation indices, suggesting time-delayed responses to habitat fragmentation, and that the effects of fragmentation magnify over time. The estimated time-delayed response to habitat fragmentation varied depending on the landscape metric and taxa. These findings underline the evidence of extinction debt found in Chapter II. Generally, the estimated duration of the delayed response to habitat fragmentation was shorter for mammals than for birds. This is likely due to the hunting pressure that mammals experience in fragmented landscapes, which makes them more vulnerable to extinction. This chapter suggests that habitat fragmentation negatively affects bird and mammal communities, but that its impacts may take some time

to manifest. Neglecting the long-term effects of habitat fragmentation may therefore lead to erroneous conclusions regarding the effects of land-use change on biodiversity.

Research Question III: What are the direct vs. indirect effects of land-use change on species' populations?

In Chapter IV, I provided answers to this question by predicting changes in giant anteater occupancy over time as a response to land-use change. Comparing the area in which occupancy decreased with the area affected by agricultural expansion enabled isolating direct from indirect effects of land-use change. Results indicated that anteater occupancy decreased by up to 84% between 1985 and 2015, especially after 2000 when rapid agricultural expansion occurred. Anteater occupancy declined over an area almost twice as large as the area directly affected by agricultural expansion. This suggests that land-use change has important indirect effects that contribute to population declines, for instance, through habitat fragmentation and edge effects. In this chapter, I highlighted areas where anteater populations declined and thus, areas where population extinctions are more likely to occur in the future.

Research Question IV: How does past and recent deforestation affect species at the population and individual level?

In Chapter V, I assessed the effects of past and recent deforestation on collared peccaries at 1) the population level by using occupancy models and 2) the individual level by using indices of physiological stress. At the population level, peccary occupancy was highest in remote areas with high forest cover. Recent deforestation had a higher effect on peccaries than past deforestation. At the individual level, food availability from croplands had the highest correlation with physiological stress levels, whereas forest loss or hunting pressure did not influence stress levels significantly. Results from this chapter suggest that peccaries respond quickly to land-use change and that they disappear as deforestation progresses, most likely due to the combination of habitat loss and hunting pressure. In this chapter, I provided a thorough understanding of the effects of past and recent deforestation on biodiversity by, for the first time, combining occupancy models with indices of physiological stress.

2 Cross-cutting insights

When synthesizing across the individual chapters of this dissertation, four cross-cutting insights emerged. These four insights contributed to better understanding the effects of past and contemporary land use on biodiversity in the Argentine Dry Chaco, and to identify the impacts of land-use change on biodiversity before local extinctions occur.

First, past landscape patterns had a substantial influence on contemporary biodiversity patterns, emphasising the importance of considering past land use data in biodiversity studies. Contemporary bird and mammal communities were strongly influenced by past landscape patterns (Chapter II & III), indicating time-delayed responses to land-use change and evidence of an extinction debt in the Argentine Dry Chaco. Chapter III further revealed that such time-delayed responses were due to habitat fragmentation, rather than to habitat loss. Most research that investigated time-delayed responses to land-use change focussed on temperate regions, in comparison to tropical and subtropical areas (Figueiredo *et al.* 2019; Lira, de Souza Leite & Metzger 2019). In addition, there has been a strong focus on plants (Figueiredo *et al.* 2019; Lira, de Souza Leite & Metzger 2019). Most of the studies carried out in tropical areas also found evidence of extinction debt (Metzger *et al.* 2009; Wearn, Reuman & Ewers 2012; Uezu & Metzger 2016), however, they did not provide detailed information regarding the differences in the relaxation time between habitat loss and habitat fragmentation. Past landscape patterns not only influenced species communities but also populations. Chapter IV highlighted areas where giant anteater population declines occurred due to land-use change, and it showed how combining past landscape data with occupancy models enabled isolating direct from indirect effects of land-use change.

Second, indirect effects of land-use change can have considerable consequences on biodiversity (Brook, Sodhi & Bradshaw 2008). Chapter IV showed that such indirect effects include threats such as hunting, road kills, or fire risk and can exert a major pressure on biodiversity in areas affected by land-use change. The interaction between land-use change and other threats seemed to be particularly important for mammals, as demonstrated by previous studies (Cullen Jr, Bodmer & Pádua 2000; Peres 2001; Tabarelli, Da Silva & Gascon 2004; Corlett 2007; Romero-Muñoz *et al.* 2019) but also by this thesis. Indeed, Chapter II showed that the time delay to extinction after habitat fragmentation was shorter for mammals than for birds, likely due to the high hunting pressure that mammals experience in fragmented landscapes as an indirect effect of land-use change. For instance, collared peccaries disappeared very fast in areas affected by deforestation, due to the combined effect of habitat loss and hunting pressure along forest edges (Chapter V). Additionally, Chapter

III indicated that habitat loss can cause the removal of individuals directly. However, road kills or fires, which often occur in areas affected by land-use change, may also contribute to anteater population declines. Overall, the results from these chapters suggest that such interactions may be responsible for short-term extinctions.

Third, forests are of utmost importance for biodiversity in the Argentine Dry Chaco. All chapters emphasized that a decrease in the deforestation rates in the region is urgently needed to avoid further biodiversity loss, and that deforested areas should be restored. Chapters II and III showed that the loss and fragmentation of forest was a major cause of species extinctions. Chapter II additionally highlighted that forest loss and fragmentation may also cause the extinction of species that are not considered to depend on forest and that can handle certain levels of anthropogenic disturbance. Those extinctions may however occur with a time delay. Previous studies have demonstrated that giant anteaters are positively associated with edges between forests and natural open areas (Medri & Mourão 2005; Desbiez & Medri 2010). Nevertheless, this thesis showed that forest cover had the strongest influence on anteaters (Chapter III), highlighting the importance of continuous forest to sustain species populations. Finally, while it has been reported that collared peccaries occur in a wider range of forest covers than other species of peccaries (Altrichter & Boaglio 2004), the results from Chapter V indicated that collared peccaries are rarely found in areas with low forest cover, and that they quickly disappear as deforestation progresses.

Fourth, the approaches developed in this thesis facilitate identifying the impacts of land-use change at an early stage, before local extinctions occur. For example, Chapter II identified when species are more likely to go extinct. Most importantly, the spatially explicit approaches presented in Chapters II and IV allowed identifying areas where population and species extinctions are more likely to occur, which is highly relevant for conservation planning. In addition, Chapter III indicated how species extinctions can be avoided, for example through restoration activities aimed at improving connectivity between forest patches. Finally, Chapter V took a step further by investigating the effects of land-use change at the individual level, at which immediate effects of deforestation can be identified when species show time-delayed responses.

Another common thread through all my four core chapters is that extensive biodiversity datasets, land-cover data with high temporal and spatial resolution, and novel statistical approaches were used to provide a more nuanced picture of species and populations at risk. This was particularly the case for Chapters III, IV and V which employed occupancy models.

These models are increasingly important in ecology and conservation due to their ability to account for imperfect detection, which is crucial when working with elusive or scarce species such as forest-dependent species (MacKenzie *et al.* 2002; Guillera-Arroita 2017). Chapter V included a particularly novel application of such models, as I combined them with indices of physiological stress. This approach enabled the assessment of the impacts of deforestation at both the population and individual level.

3 Future research

With this thesis, I sought to contribute to a better understanding of the responses of biodiversity to land-use change, and to provide insights regarding where, when and why extinctions are more likely to occur. However, several interesting directions for future research emerged during the course of this thesis that were beyond the scope of this dissertation.

First, I investigated the immediate and time-delayed effects of land-use change on biodiversity in dynamic landscapes. I assessed differences between taxa (birds vs. mammals), and between species with different habitat requirements (forest-dependent species vs. entire community). Other life-history traits such as mobility, longevity, or diet, can have an influence on the magnitude and duration of time delays (Kuussaari *et al.* 2009; Figueiredo *et al.* 2019; Lira, de Souza Leite & Metzger 2019). Unfortunately, how species traits affect time-delayed responses is poorly understood (Figueiredo *et al.* 2019), and thus, further research is needed to understand the variation in time-delayed responses across different functional groups. Moreover, given the importance of the interaction between land-use change and hunting in the Argentine Dry Chaco, understanding how responses to land-use change differ between hunted vs. non-hunted species can provide insights into the influence of hunting on the duration of the time delay.

Second, the spatially explicit approach presented in Chapter II allowed quantifying the number of species predicted to go extinct due to past land-use change. However, this approach did not determine which species are subject to a delayed extinction. Such information would provide valuable information for conservation management, as species-specific conservation measures can be implemented depending on the probability of extinction of a given species. Previous studies have estimated extinction debt for single species by investigating the relationship between past and contemporary landscape patterns and occurrence of different species (Piha, Luoto & Merilä 2007; Saito, Furukawa &

Koyanagi 2016). However, community-level studies that directly identify which species are affected by extinction debt are lacking.

Third, expansion of extensive grazing during the last decades has led to widespread forest degradation in the Argentine Dry Chaco (Grau, Gasparri & Aide 2008). This thesis focused on the effects of forest loss and fragmentation only; including forest degradation would provide a more nuanced picture of the effects of land-use change on biodiversity. However, mapping forest degradation by using satellite imagery is challenging (Hirschmugl *et al.* 2014), and as a result, no suitable data was available to investigate the effects of past and contemporary forest degradation on biodiversity. Including such information when it becomes available can provide a means to assess biodiversity responses to habitat loss, fragmentation *and* degradation.

Fourth, I developed several approaches that allow identifying the impacts of land-use change on biodiversity at an early stage. Applying these novel approaches to other species and regions would indicate their effectiveness in other systems and can potentially guide conservation management in other deforestation frontiers where species and populations are facing extinction. In addition developing some of the approaches of this dissertation further may enhance their accuracy. For instance, integrating the approach from Chapter II in an occupancy framework would allow to account for imperfect detection, and thus to ensure that extinction debt is not underestimated.

Lastly, this thesis relied on extensive field datasets which facilitated investigating the effects of land-use change at the community, population and individual level. While land-cover data is relatively easy to obtain by classifying satellite imagery, gathering biodiversity data is often more costly and time consuming, especially in remote areas like the Gran Chaco. Nevertheless, collecting new field data will be valuable for further research. For instance, multi-year biodiversity data can potentially provide better estimates of population trends, as well as to estimate population parameters such as survival and colonization probabilities by implementing multi-season modelling approaches. Similarly, identifying individuals by non-invasive genetic sampling (e.g., DNA extracted from feces or hair) will provide the means to use alternative statistical models, such as spatial-capture-recapture models, and thus, to directly estimate abundance. Additionally, fecal samples can be used to determine the gender of individuals, and thus to assess differences in the physiological response to deforestation between males and females.

4 Conservation implications

Considering the current and predicted future global demand for agricultural products (Tilman *et al.* 2011), and the potential of the Argentine Dry Chaco for agricultural expansion (Lambin *et al.* 2013), there is a great need to understand how deforestation affects biodiversity. From a conservation perspective, timely action is crucial to prevent biodiversity loss. Thus, detecting the impacts of land-use change at an early stage is needed to know where, when and how to act. Most importantly, the maps generated as part of this thesis, depicting population declines and extinction debt across the Chaco, provide valuable information which can be used to halt those extinctions. The results from this thesis are summarized into four specific recommendations. First, in areas where populations are increasing or stable, or where species extinctions are not predicted to occur, pro-active conservation strategies should be prioritized (e.g., protection of forested areas). Second, reactive management such as restoration should be implemented in areas where populations are already declining, or where species extinctions are more likely to occur. Moreover, restoration activities aimed at avoiding the payment of the extinction debt should be directed towards increasing connectivity, rather than increasing the amount of forest area, as forest fragmentation seemed to be the main driver of extinction debt. Third, in areas that seem untransformed but where population declines are observed (i.e., areas affected by indirect effects of land-use change), other measures such as fire regulation or enforcing anti-poaching laws may be more effective. Finally, the results of this thesis also suggest that some species in the Argentine Dry Chaco respond to land-use change immediately. This is the case for the collared peccary, which is quickly disappearing from Chacoan landscapes due to habitat loss and hunting pressure. Conservation of such species should be prioritized, as the window of time for averting local extinction is likely to be shorter.

Several conservation measures have already been implemented in the Argentine Dry Chaco with the aim of decreasing deforestation and conserving biodiversity, and some of the results of my work have entered relevant policy discussions. For instance, the National Forest Law that was passed in 2007 aims to promote forest conservation and regulate agricultural expansion. For this purpose, the forest areas are zoned into three categories: category I (*red*) where deforestation is not allowed, category II (*yellow*) where sustainable uses are allowed, and category III (*green*) where deforestation is allowed. Unfortunately, deforestation is still an ongoing threat to the Argentinian Chaco forests, even in areas categorised as *red* (Sans *et al.* 2018).

Another mechanism that has been implemented in the Argentine Dry Chaco is the Payment for Ecosystem Services (PES), which compensates landowners for activities that contribute to a sustainable use of the forest, including conservation, restoration, silviculture and silvopasture (Núñez-Regueiro *et al.* 2019). Considering the main conservation recommendations of this thesis, the PES program might be a useful tool to implement restoration activities in areas where future extinctions are more likely to occur. However, previous research in the Argentine Chaco has indicated that landowners are less likely to enroll in PES programs to undertake restoration than to undertake activities that promote sustainable forest management and conservation (e.g., silvopastures) (Núñez-Regueiro *et al.* 2019). Increasing incentives for long-term enrollment in restoration projects is therefore needed. Additionally, disseminating the results from this thesis among different local stakeholders would be key for incorporating such results into the PES program. Some results have already been presented to stakeholders from Argentina as part of a larger project namely PASANOA (Pathways to Sustainable Land Management in Northern Argentina). For instance, results from Chapter II and III have already been presented to representatives of the Argentinian government and several non-governmental organizations (NGOs) in Buenos Aires, and they will be translated into policy recommendations and released as policy briefs with the aim of reaching government policy makers.

Through the work developed in this thesis, I also contributed to other studies under the PASANOA project, in which trade-offs between agricultural intensity and biodiversity were assessed by using a multi-species occupancy framework, thus providing information regarding the conservation value of different agricultural systems. These results have not only been presented to government bodies, but also to local landowners and producers with the aim of obtaining their opinions, comments and perceptions regarding the current and future state of the Chaco. Finally, a workshop aimed at conserving the Argentine Chaco forests will take place in Resistencia (capital of the Chaco province) in August 2019, and the conservation recommendations of this thesis will be presented to different NGOs with the aim of guiding policy makers.

The IPBES has recently documented a global crisis of natural ecosystems, and urgent action is needed to ensure a future for the planet and its biodiversity (Díaz *et al.* 2019). Particularly tropical and subtropical dry forests are under pressure of multiple threats, mainly caused by human activities (Miles *et al.* 2006). Unfortunately, few people are aware of their importance

for biodiversity. The results of my thesis showed that biodiversity in the Gran Chaco, the largest tropical dry forest in the world, has greatly been affected by land-use change and hunting pressure, and that those threats are responsible for driving species to extinction. The world's human population is growing progressively, resulting in a surging demand for agricultural products and further transformation of natural ecosystems (Tilman *et al.* 2011; Gerland *et al.* 2014). The high deforestation rates and associated species extinctions that we observe today in the Chaco may therefore move to other tropical dry forests in the future, for example in Africa or Asia. To avoid local extinctions, more attention should be paid to this threatened ecosystem, and in particular, to understanding the immediate and time-delayed effects of deforestation on biodiversity.

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Publikationen

PEER-REVIEWED JOURNAL ARTICLES

Published or accepted manuscripts

[3] **Semper-Pascual, A.**, Macchi, L., Sabatini, F.M., Decarre, J., Baumann, M., Blendinger, P.G., Gómez-Valencia, B., Mastrangelo, M.E. & Kuemmerle, T. (2018) Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. *Journal of Applied Ecology*, 55, 1218-1229.

[2] **Semper-Pascual, A.**, Decarre, J., Baumann, M., Busso, J.M., Camino, M., Gómez-Valencia, B. & Kuemmerle, T. (2019) Biodiversity loss in deforestation frontiers: Linking occupancy modelling and physiological stress indicators to understand local extinctions. *Biological Conservation*, 236, 281-288.

[1] Kuemmerle, T., Altrichter, M., Baldi, G., Cabido, M., Camino, M., Cuellar, E., Cuellar, R.L., Decarre, J., Díaz, S., Gasparri, I., Gavier-Pizarro, G., Ginzburg, R., Giordano, A.J., Grau, H.R., Jobbágy, E., Leynaud, G., Macchi, L., Mastrangelo, M., Matteucci, S.D., Noss, A., Paruelo, J., Piquer-Rodríguez, M., Romero-Muñoz, A., **Semper-Pascual, A.**, Thompson, J., Torrella, S., Torres, R., Volante, J.N., Yanosky, A. & Zak, M. (2017) Forest conservation: Remember Gran Chaco. *Science*, 355, 465-465.

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[6] **Semper-Pascual, A.**, Decarre, J., Baumann, M., Camino, M., di Blanco, Y., Gómez-Valencia, B. & Kuemmerle, T. (under review) Using occupancy models to assess direct and indirect impacts of land-use change on species' populations. *Biodiversity and Conservation*.

[5] **Semper-Pascual, A.**, Burton, C., Baumann, M., Decarre, J., Gavier-Pizarro, G. I., Gómez-Valencia, B., Macchi, L., Mastrangelo, M.E., Pötzschner, F., Zelaya, P.V. & Kuemmerle, T. (submitted). Contemporary or past habitat fragmentation: good or bad for biodiversity? *Ecology Letters*

[4] Macchi, L., Decarre, J., Goijman, A. P., Mastrangelo, M. E., Blendinger, P. G., Gavier-Pizarro, G. I., Murray, F., Piquer-Rodriguez, M., **Semper-Pascual, A.**, & Kuemmerle, T. (submitted) Trade-offs between biodiversity and agriculture are moving targets in dynamic landscapes. *Nature Ecology and Evolution*.

CONFERENCE CONTRIBUTIONS

[16] **Semper-Pascual, A.**, Macchi, L., Sabatini, F.M., Decarre, J., Baumann, M., Blendinger, P.G., Gómez-Valencia, B., Mastrangelo, M.E. & Kuemmerle, T. (2018). Time-delayed responses to land-use changes reveal a window of opportunity for biodiversity. *28th International Congress for Conservation Biology*, Cartagena, Colombia

[15] **Semper-Pascual, A.**, Decarre, J., Baumann, M., Camino, M., di Blanco, Y., Gómez-Valencia, B. & Kuemmerle, T. (2108). Stark increase in potential sink

habitat for Giant Anteaters in the Argentine Dry Chaco due to land-use change. *IUFRO Conference*, Posadas, Argentina

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Eidesstattliche Erklärung

Hiermit erkläre ich, die vorliegende Dissertation selbstständig und ohne Verwendung unerlaubter Hilfe angefertigt zu haben. Die aus fremden Quellen direkt oder indirekt übernommenen Inhalte sind als solche kenntlich gemacht. Die Dissertation wird erstmalig und nur an der Humboldt-Universität zu Berlin eingereicht. Weiterhin erkläre ich, nicht bereits einen Doktortitel im Fach Geographie zu besitzen. Die dem Verfahren zu Grunde liegende Promotionsordnung ist mir bekannt.

Asunción Semper-Pascual

Berlin, den 30.08.2019